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The phi complex as a neuromarker of human social coordination

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Many social interactions rely upon mutual information exchange: one member of a pair changes in response to the other while at the same time producing actions that alter the behavior of the other. However, little is known about how such social processes are integrated in the brain. Here, we used a specially designed dual-electroencephalogram system and the conceptual framework of coordination dynamics to identify neural signatures of effective, real-time coordination between people and its breakdown or absence. High-resolution spectral analysis of electrical brain activity before and during visually mediated social coordination revealed a marked depression in occipital alpha and rolandic mu rhythms during social interaction that was independent of whether behavior was coordinated or not. In contrast, a pair of oscillatory components (phi1 and phi2) located above right centro-parietal cortex distinguished effective from ineffective coordination: increase of phi1 favored independent behavior and increase of phi2 favored coordinated behavior. The topography of the phi complex is consistent with neuroanatomical sources within the human mirror neuron system. A plausible mechanism is that the phi complex reflects the influence of the other on a person’s ongoing behavior, with phi1 expressing the inhibition of the human mirror neuron system and phi2 its enhancement.

brain oscillations | electroencephalography | mirror neuron system | phi rhythm | coordination dynamics

Two anatomically overlapping yet functionally distinct systems in the brain have been identified when we interact with others. The first, historically called the motor preparation system, consists of corticospinal circuitry that includes the premotor cortex, the supplementary motor area, and parts of the inferior parietal cortex. This system is deemed responsible for implementing the intention to realize one’s own actions. The second, the mirror-neuron system, allows for the imitation of others’ movements with and without vision of each other’s actions. The mirror-neuron system is consistent with neuroanatomical sources within the human mirror neuron system. A plausible mechanism is that the mirror-neuron system reflects the influence of the other on a person’s ongoing behavior, with phi1 expressing the inhibition of the human mirror neuron system and phi2 its enhancement.

Coordination dynamics to identify neural signatures of effective, real-time coordination between people and its breakdown or absence. High-resolution spectral analysis of electrical brain activity before and during visually mediated social coordination revealed a marked depression in occipital alpha and rolandic mu rhythms during social interaction that was independent of whether behavior was coordinated or not. In contrast, a pair of oscillatory components (phi1 and phi2) located above right centro-parietal cortex distinguished effective from ineffective coordination: increase of phi1 favored independent behavior and increase of phi2 favored coordinated behavior. The topography of the phi complex is consistent with neuroanatomical sources within the human mirror neuron system. A plausible mechanism is that the phi complex reflects the influence of the other on a person’s ongoing behavior, with phi1 expressing the inhibition of the human mirror neuron system and phi2 its enhancement.

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Abbreviations: EEG, electroencephalogram; LC, liquid crystal; CV, circular variance.

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Fig. 1. The experimental setting and behavioral findings. Visual contact between subjects is manipulated by turning on (A) and off (B) a liquid crystal screen. (C) Distribution of trials for all eight pairs of subjects, arranged in increasing degree of coordination. An index (γ<sub>CV</sub>) based on circular variance was used to assess the strength of coordination. Orange bars represent unsynchronized behavior (γ<sub>CV</sub> < 0.03); green bars are from synchronized trials (γ<sub>CV</sub> > 0.73). Dark and light green signify in-phase and anti-phase synchronization, respectively. Yellow bars represent transient behavior. The overall relative phase distributions for all trials corresponding to the vision-off and vision-on segments are shown in D and E, respectively. By using similar color coding as in C, further decompositions into synchronized (F), transient (G), and unsynchronized (H) trials are displayed.

that enabled us to observe evolving patterns of behavioral and brain activity. Social interactions (“vision-on,” 20-s duration) were framed by two 20-s control periods (“vision-off”) during which participants’ sight of each other was blocked. Vision was controlled by using a liquid crystal (LC) screen panel, interposed between participants, the opacity of which could be electronically switched on and off (see Fig. 1 A and B).

Vision of the other created the opportunity for a transition from independent to coordinated behavior: accordingly, the distribution of the relative phase of finger movements during vision-on (Fig. 1E) showed some concentration at 0 (modulo 2π), and π (modulo 2π), expressing tendencies for synchronizing in-phase (fingers of both participants reaching their peak flexion at the same time) and anti-phase (fingers of one participant reaching peak extension at the same time that the other reaches peak flexion). This relative phase concentration was absent during vision-off (Fig. 1D).

Trials were classified into three categories: fully synchronized, transiently synchronized, and unsynchronized, quantitatively verified by using an index of synchronization γ<sub>CV</sub> (see Materials and Methods). Social coordination was defined when the relative phase of the finger movements entered a stable phase-locked state shortly after visual contact (<2 s) and persisted over the entire period of visual contact. Transient synchronization was defined when brief episodes of phase locking were observed during the period of visual contact but were not maintained throughout the period. Unsynchronized behavior was defined by the persistent absence of phase locking across the entire period of visual contact. Fig. 1C shows the distribution of the trials based on the three categories of behavior: synchronized, transient, and unsynchronized. Trials of fully synchronized behavior accounted for 25% of all of the trials (Fig. 1F). Transient phase locking was observed in 37% of the trials (Fig. 1G). Both synchronized and transient trials showed tendencies toward in-phase and anti-phase patterns, reminiscent of many studies of rhythmic sensorimotor coordination in individual subjects (e.g., refs. 32 and 57–65). Unsynchronized trials comprised 38% of the total and were characterized by a complete absence of phase-locking tendencies (Fig. 1H). No phase attraction means that subjects essentially retained their own rhythm and were unaffected by the visual input of the other’s movements.

Coordination behavior was verified visually and numerically by using a synchronization index based on the relative phase circular variance (66). This index is a unit-normalized number, with 0 describing the absence of synchronization and 1 describing full synchronization. Synchronized trials had an index >0.73 whereas unsynchronized ones had an index of <0.03. Transient behavior was in between, with synchronization index values ranging from 0.03 to 0.75 (Fig. 1G). Notice that the index is a measure of the net strength of the interaction arising from the individual intrinsic dynamics (reflected in the frequency and amplitude of movements chosen before visual contact) and the mutual coupling.

Neural correlates of synchronized and unsynchronized behaviors were sought by using high-resolution spectral analysis (0.06-Hz steps). The rationale was that emergent coordinative behaviors, whether synchronized or unsynchronized, would be sustained by at least one of the subjects in the pair. Accordingly, we expected to identify neural signatures of social coordination by observing corresponding EEG spectral changes. By using the visualization method described in Materials and Methods, three categories of spectra with distinct topography were identified in the 7.5- to 13-Hz range (Fig. 2A and B): alpha (mean frequency of 10.61 Hz), mu (mean frequency of 9.63 Hz), and a lateralized centro-parietal component that we call phi (spanning the range 9.2–11.5 Hz; Fig. 2B). In 11 subjects, separable peaks were observed for at least one of the three brain rhythms (Fig. 2B).
In particular, phi was observed in all 11 subjects, 10 with right and 1 with left lateralization. Phi appeared at a single brain location but typically involved a double peak in the spectral domain (Fig. 4 A and B).

Although alpha and mu showed a significant decrease (alpha, −30.4%; mu, −20.1%) during visual contact as compared with before visual contact (alpha at POz, Z = −2.67, P < 0.008; mu at FCz, Z = −2.1, P < 0.036; Fig. 2C), neither rhythm was specifically modulated by the strength of the coordination per se. Specifically, these rhythms displayed intermittent bursting before and after visual contact and were suppressed during vision (Fig. 3).

In contrast, the phi complex was highly sensitive to the characteristics of social coordination achieved during visual contact. Increase of the first component was specific to unsynchronized behavior; increase of the second component was specific to synchronized behavior (Fig. 4 C and D).

In a number of cases during which the spectral amplitude of mu and/or alpha was small, we were able to identify changes in the dynamics of the phi complex associated with changes in behavioral coordination (Fig. 5). Such cases support the causality between the phi complex and social coordination.

**Discussion**

Consistent with previous studies of behavior alone (27, 55), spontaneous coordination in the form of synchronized behavior was observed between participants during visual contact even though no instruction to coordinate was given. Vision of the other’s movements created an opportunity to couple, often inducing a transition from independent to coordinated behavior. Interestingly, the discrete set of stable-phase relations observed (in-phase and anti-phase) indicated that basic symmetries are at work even between two people (28, 60, 67). For social coordination qua phase-locking to occur, at least one of the participants has to be influenced by vision of what the other is doing. In neural terms, the mirror-neuron system must effectively influence the motor cortex of at least one participant (68, 69). In contrast, when no phase-locking tendency is observed individual behaviors (“intrinsic dynamics”) predominate (33), presumably by enhancing activity in the premotor system or by inhibiting the mirror-neuron system. Our results suggest that phi1 reflects the inhibition of the mirror-neuron and/or the enhancement of intrinsic premotor activity, whereas phi2 reflects the enhancement of the mirror-neuron system and/or the inhibition of intrinsic premotor activity. Potential sources for the centro-parietal phi complex include areas reported to belong to the human mirror-neuron system, in particular parietal areas and the superior temporal sulcus (4, 5, 9, 10, 17, 70–81). The presence of a complex formed by two distinct peaks is an unusual spectral feature of human EEG. It could express the activation of largely overlapping networks (e.g., motor preparation and mirror neuron systems) so that the observed proximity in both the spectra and topography is attributed to the common parts; or it could indicate a frequency shift of a single oscillation because of coupling with remote processes.

The present results show that, although mu and alpha are consistently depressed by the perception of the other’s movement, they are insensitive to social coordination or its absence. Both mu and alpha rhythms have been described as functional correlates of resting brain states and arise from the hyperpolarization of thalamo-cortical relay cells (82). Alpha desynchroni-
They constituted eight pairs: four gender-mixed; three male–female; and one female–female. All were right-handed on the basis of self-report. They had normal or corrected-to-normal vision and reported no history of neurological disease. The protocol was approved by the Florida Atlantic University ethical board and was in agreement with the Declaration of Helsinki. Informed consent was obtained from all subjects.

**Task.** Pairs of subjects sat in front of each other while executing self-paced rhythmic finger movements during one-minute trials. An LC screen (Alumiglass, FL) with switchable opacity (switching time <1.2 ms) was placed between subjects to control vision of the other’s motion. A trial consisted of three successive phases each lasting 20 s: before-vision, with the LC screen opaque (Fig. 1A), during-vision, with the LC screen transparent (Fig. 1B), and after-vision, with the screen back to opaque again (Fig. 1A). The LC screen was electronically controlled by means of a computer running the Experimental Run Time System (ERTS; Berisoft, Germany) software for optimal timing accuracy. Subjects were instructed to adopt the movement frequency that they felt most comfortable with and to maintain the fixation over a central spot on the LC screen. When the screen was transparent, the spot was in the same azimuth as the hand of the other participant. EEG artifacts induced by posture or finger movements were minimized before each trial. A trial started with two auditory cues presented in succession, one to each subject, signaling the respective recipients to commence rhythmically moving their index fingers at their preferred frequency and amplitude. The auditory warning cues were delivered through separate ear pieces 2 s (±0.5 s, random distribution) and 1 s (±0.5 s, random distribution) before the onset of the first 20-s period. The variable delay set a random initial relative phase between subjects and prevented common phase priming in the movements. The experiment consisted of 36 trials, with at least a 30-s rest between trials.

**EEG Recording.** The experiment was conducted in a sound-proof Faraday chamber. Dual-EEG was recorded by using two 60-channel EEG caps with Ag-AgCl electrodes (Falk Minow Services, Germany) arranged according to the 10% system (97) including midline and rows 1–8. The signals were fed to a single amplifier (Synamp2; Neuroscan, TX) equipped with two distinct referential montages. This specially designed dual-EEG system ensured no delays between the EEGs acquired from each subject and allowed precise analyses of cortical activity. EEG signals were measured with the respective grounds located at FPz sites and the references at the corresponding linked mastoids. Impedances were maintained below 10 kΩ (98). The signals were analog filtered (Butterworth, bandpass from 0.05 Hz (−12 dB per octave) to 200 Hz (−24 dB per octave), amplified (gain of 2,010) and digitized at 1,000 Hz with a 24-bit ADC in the range ±950 μV (vertical resolution of 0.11 nV).

**Movement Recording.** For finger movement data, angular change at the metacarpophalangeal joint was recorded by means of light single-axis goniometers (Biometrics, Ltd., U.K.) affixed to the right index finger of each subject. These signals were acquired through the high level port of the Neuroscan Synamp 2 bioamplifier, with an online bandpass filtering at a common EEG analog filter setting (0.05–200 Hz).

**Behavioral Analysis and Statistics.** Movement data were preprocessed by using a digital low-pass filter (Butterworth; 10 Hz, 24 dB) applied in a two-pass recursive manner to achieve zero-phase shift. The relative phase between the fingers was computed by using the continuous Hilbert transforms of the mean-centered time series. On the basis of the movement profiles during the visual contact period, the trials were initially classified by three experts into three categories: synchronized, transiently...
synchronized, and unsynchronized trials. The classifications were further refined and numerically checked by using the synchronization index $\gamma_{CV}$, based on the circular variance (CV) (66) of the relative phase. Note that this measure is sensitive to variations of the phase of the time series and not to the amplitudes. For $N$ data points, the index is defined as

$$\gamma_{CV} = \frac{1}{N} \left| \sum_{k=1}^{N} e^{i(\theta_k^{(1)} - \theta_k^{(2)})} \right| = 1 - CV,$$

where $\theta_k^{(1)}$ and $\theta_k^{(2)}$ are the Hilbert phases for the subject pair at time $k$ and $CV$ is the circular variance of the differences $\theta_k^{(1)} - \theta_k^{(2)}$. If the phases follow each other closely at all times (highly synchronized), $\gamma_{CV} \approx 0$ for some constant $\delta$, and $\gamma_{CV}$ is close to one. For fully unsynchronized and uncoupled systems, $\gamma_{CV}$ tends to 0. A lower bound and an upper bound for $\gamma_{CV}$ were used to discriminate between synchronized and unsynchronized trials, respectively. Note that the index is a measure of the net strength of the interaction arising from the individual intrinsic dynamics (reflected in the frequency and amplitude of movement chosen before visual contact) and the mutual coupling.

**EEG Spectral Analysis.** Classical studies of EEG oscillations are often performed (i) at low spectral resolutions by using fast Fourier transform (FFT) on samples of a few hundreds of milliseconds; (ii) within large frequency bands (typically 2–3 Hz in the alpha range); and (iii) without access to the interindividual variability in the frequency of the rhythms. Our paradigm allowed us to investigate rhythms over a period of 16.5 s from each 20-s segment of a trial (a 3-s transient at the onset and a 0.5-s transient at the end were removed as the brain activity was expected to be nonstationary near these boundaries), resulting in a spectral resolution of 0.06 Hz. Single trials were tapered with a Tukey window (10%), and discrete Fourier transforms (DFT) were used to estimate amplitude spectra. For display purposes, Ouyang et al. (97) were refined and numerically checked by using the continuous wavelet transform (CWT). For the mother function of the transform, we chose the complex Morlet wavelet $\psi(x)$

$$\psi(x) = \sqrt{\pi f_0} e^{i2\pi f_0 x} e^{-x^2},$$

where $f_0$ is the center frequency and $f_0$ is frequency bandwidth. The Morlet wavelet is a complex sinusoidal function tapered with a Gaussian window and is optimal for sinusoidal-shaped oscillations such as alpha. It can also detect spectral components of different morphologies such as mu but with lower spectral definition and leakage of parts of the power into additional/other components.

**EEG Artifacts.** Eye blinks are large-amplitude EEG components whose waveforms resemble positively skewed Gaussians, sometimes associated with final undershoots. The typical duration of an eye blink is 200–400 ms, and its spectral signature spans the delta and theta range (101, 102), with most of the energy residing below 5 Hz. Muscle artifacts arise from the fluttering of the electrodes in the vicinity of active neck and face muscle groups and span the frequency range from the beta band up to $\approx$500 Hz (103, 104). The spectral characteristics of these two contaminants (eye blinks and muscle artifacts) have no overlap with the frequency bands investigated here. In agreement with Wallstrom’s report (105) of induced second-order artifacts when correcting for primary contaminants (and especially in the alpha band), we did not employ correction techniques (e.g., regression, filtering, and decomposition) on the data.

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