EEG Coordination Dynamics: Neuromarkers of Social Coordination

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Summary: The aim of this chapter is to present a framework of EEG Coordination Dynamics based on rhythmical entrainment of brain activity. The interest of continuous brain~behavior¹ analysis is underlined, and its principles are illustrated with results from a dual-EEG experiment of spontaneous social coordination.

1 Introduction

At the source of Coordination Dynamics is the will to identify organizing principles in (living) systems transcending both the specifics of their substratum and their levels of description. An example of such research in the wake of Kelso is movement coordination, which has been studied theoretically [29, 41, 17, 25, 34, 24, 1, 35] and empirically; at the behavioral [37, 38, 36, 33, 56, 65, 11, 13, 8, 20] and brain level [40, 61, 43, 26, 49, 48, 52, 32], in single subjects but also in paired individuals [22, 53, 60]. In the present chapter, we present ongoing research on interpersonal coordination coupled by visual information. Brain dynamics was recorded through a specially designed dual-EEG system while vis-'vis pairs of subject performed and simultaneously observed self-paced finger oscillations. A variety of behaviors emerged from this situation, ranking from independent, to transiently locked, to stable in-phase and antiphase synchronous. Our aim was to combine Coordination Dynamics and EEG to uncover the neural signatures of individual and social behaviors.

In a first movement, we will describe limitations of classical EEG approaches to meet some of the requirements of Coordination Dynamics, as well as efforts taken to overcome them. In a second movement, we will detail interpersonal coordination dynamics at the behavioral level and isolate

¹ The tilde symbol (∼) was introduced by Kelso and Engström to indicate complementary pairs, i.e. "modes of a dynamical system that is capable of moving between boundaries even as it includes them" ([42], p.9).

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homogenous classes of coordination. In a third movement, we will present a description of brain dynamics in which the neuronal components are delimited but neuronal coordination is not yet apprehended. Ultimately, we will chart strategies to capture interactions between neuronal components across brains, so as to reveal mechanisms through which the social level could emerge.

2 EEG Coordination Dynamics

On one side, we have EEG, a neuroimaging method known for its temporal resolution and commonly used to relate brain and behavior. On the other side, we have Coordination Dynamics, which seeks to reconcile levels of organization in biological systems and study the temporal evolution of coordination variables derived from the dependency of elements within and/or between the behavior and brain levels. The concord sounds immediate, however convergence of both field into an integrated framework is not as straightforward as one would think.

A classical approach to EEG analysis consists of extracting recurring dynamics through averaging of time-locked brain activity in paradigms of repeated events. From the viewpoint of coordination dynamics, qualitative changes in the system's time-course are of major interest to understand its dynamical skeleton and associated neural correlates. A first problem is that such impromptus of behaviors are difficult to grasp with this classical EEG approach. Their recurrence and temporal definition may not be sufficient to lead to adequate event-related dynamics. Even when such conditions are met, a second problem comes into play: averaged signals are not always faithful representations of continuous brain dynamics. Key to those two problems, the recursive dynamics derived from classical EEG analysis does not have an inscription in the continuous dimension in which the behavior lives (see Sec. 2.2). Taken together, those limitations lead us to an alternative strategy, i.e. not to use EEG averaging but to develop ways to study both brain and behavior dynamics continuously. A tractable issue with EEG signal-to-noise ratio is to maximize the signal by resorting to rhythmic entrainment of brain dynamics.

2.1 Impromptus of behaviors

Because of the complexity of the brain and of the continual spatio-temporal overlap of many simultaneous ongoing processes, EEG studies of cognitive or behavioral phenomena usually consists of isolating a small fraction of task-related activity amidst a substantial amount of 'back-ground' neural noise. In addition, the signal gathers an even larger amount of instrumental and environmental recording noise. The long-established methodology of EEG analysis to deal with this unfavorable Signal-to-Noise Ratio (SNR) is to average a large number of realizations of the same event so as to cancel-out task-unrelated

oscillatory components. This is done both in the time [63, 19, 54, 14] and frequency domains [51, 3, 57, 44], and requires events to be frequent enough (typically in the hundreds) and well defined in their temporal onset (no more than a few milliseconds in jitter or uncertainty).

In parallel, the *modus operandi* of Coordination Dynamics is to stimulate qualitative changes in the collective variable. Those transitions clue the investigator toward the identification of the attractors' structure underlying the system. In practice, the collective variable is monitored continuously and its trajectory spends most of its time in one state or another, only briefly undergoing transitions. Such transition events may be too rare, and they may not have sufficiently precise temporal onset to be integrated in the classical EEG framework. Reciprocally, if attempting to read the EEG in the continuous dimension of the behavior, one is turned back to the critical issue of noise.

We conclude that EEG investigations of Coordination Dynamics tract with two distinct time scales: (1) a continuous time scale in which the behavior's collective variable evolves and changes under the constraints of some control parameters, and (2) a recursive time scale in which information-rich variability scattered within the discontinuous windows of brain activity is overwhelmed. Because of the incompatibility between those two time scales, EEG is not directly geared toward the understanding of real-time changes in brain activity that accompany real-time changes in behavior.

2.2 Recursive time and the methodology of EEG

One could however hope that selective aspects of brain dynamics would be preserved by the process of averaging. Brain activity linked to a precise event (stimulus or response), and consistent across trials would emerge and faithfully reproduce at the recursive time scale what happens over and over again at each discrete event along the continuous time scale of behavioral coordination.

The model of EEG underlying this simple view was once dominant. Its rationale was to extract event-related components (consistent positive or negative deflections phase-locked to the event reflecting cortical activation) which were obscured under a layer of additive noise. Current theories of EEG signal suggest a more complex picture involving at least both event-related activations and changes of underlying populations' phases [2, 46, 64, 16, 27], maybe additional mechanisms. In such a model, potentially large discrepancies exist between the task-related signal present in real-time, and the reconstructed dynamics estimated from averaged data (Fig. 1).

The properties of the reconstructed dynamic differ from those of the continuous dynamic. For instance in the spatial domain, maxima in topographical maps can appear at the intersection of two distinct regions which alternate over repetitions of the event (e.g. Cz maximum cumulating alternating temporal left and right temporal maxima). Another example in the temporal domain is the existence of amplitude difference in event-related dynamics which may

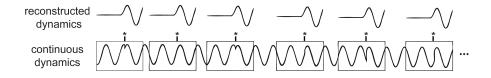


Fig. 1. Two levels of representation of brain dynamics. An event appears recurrently (stars atop second row) during the time course of the behavior and elicits phase resetting of a brain rhythm (lower row), which is hidden by the presence of noise. To identify cortical activity evoked by the event, continuous dynamics of EEG (lower row) is substituted with its event-related dynamics (upper row), the latter consisting of averaged epochs from the former in the time (as here) or frequency domain.

not express any modulation of the EEG amplitude at the continuous timescale, but rather arise from a more pronounced phase-locking to the event. Those distinct properties limit our ability to infer the continuous brain dynamics from its reconstructed dynamics.

2.3 Maximizing the signal to analyze continuous EEG: recruitment and entrainment

In the previous paragraph, we considered three kinds of EEG activities: those which continuous dynamics may be acceptably represented by the event-related dynamics, those which may be distorted and those which can simply not be handled through averaging. For the former, a possible strategy is to seed duplicates of the event-related dynamics at all appropriate moments and compare continuously the behavior with the reconstructed EEG. For the two latter, grounds for this strategy are lacking and one has to choose an alternative strategy of analyzing the EEG in continuous despite the presence of noise.

This alternative strategy requires to maximize the neural signal. A robust and lasting neural response is indispensable, and cannot be obtained with sustained sensory or motor event as they cause the brain to decrease its response through habituation [59, 45]. However, at the interface between spontaneous brain rhythms and discrete evoked responses, some robust EEG activity has been shown to emerge [28]: a rhythmical sensory or motor event will establish persistent brain activity. This is a requirement which is easily met by paradigms of Coordination Dynamics: while not requiring paradigms of rhythmic behavior [35], the framework of Coordination Dynamics has a historical predilection for oscillatory systems. With the EEG being extremely inconsistent from moment to moment (eg. Bullock et al. [9]), the rhythmic strategy attempts to force brain dynamics so that it becomes more stationary due to the periodic event (stimulus or behavior).

We distinguish two types of brain responses elicited by rhythmic events. The first is known as steady state, frequency following response or flicker phenomenon [62, 47, 28] and consists of oscillatory brain activity that resonates at the frequency of the rhythmical event. The advantage of this entrained response is straightforward: at some critical frequencies of stimulation, the amplitude of the brain's oscillatory response to periodic stimuli reaches a maximum [28, 30], i.e. the SNR is increased and task-related activity may rise above the level of background noise. A second type of brain response is the recruitment of neural activities at frequencies other than the events'. As soon as the evoked responses elicited by successive events overlap, continuous task-related neural activity occurs. Robustness is therefore achieved by persistence of a pattern of activity in the temporal domain. In addition, interactions between the events' steady-state and brain rhythms at other frequencies are expected, however such questions are a matter of very recent interest [55, 6, 10, 18], very rarely conducted on periodically forced oscillations (but see Cyetkovic et al. [15] and Thomas et al. [58]). We suggest that due to nonlinear interaction between neural populations, rhythmic events may stabilize robust brain responses in a range of frequencies, establishing the grounds for EEG coordination dynamics based on rhythmic paradigms.

3 Varieties of behaviors in spontaneous social coordination

In a study of social coordination, we put the preceding principles at work at the behavioral and brain level. Subjects (n=16, allotted to 8 pairs) performed repetitive finger movements at their preferred frequency and amplitude and were intermittently exposed to the view of each other in a session consisting of 36 trials. Visual coupling was controlled by a liquid crystal window alternating between opacity and transparency during 3 periods of 20 sec. Participants' finger movements were recorded using light single-axis goniometers affixed to their right index. The task had been developed to provide minimal inducement to the subjects' behavior, and typically resulted in a variety of patterns which seemed to carry various degrees of social valence. The first objective of this research was to classify behavioral patterns obtained during periods of social interaction. Patterns were examined by following continuously the dynamics of the behaviors' coordination variable: the relative phase between the two finger movements.

In a general sense, coordination between two oscillatory components arises as a result of their coupling, i.e. each element leaks its functional state to the other element in a way that influences the other's future state. This coupling can be a physical connection (as is the case in the interactions between neurons) but in the realm of human behavior it is also often supported by an informational connection mediated by sensory systems. In the paradigm of

social coordination developed by Kelso and collaborators [53], the primary system connecting the behavior of each subject is visual perception.

Episodes of phase-locking were observed in all pairs of subjects. They favored in-phase (both subjects flex their finger in synchrony) and antiphase coordination (one subject flexes his finger while the other extends), although a few pairs sustained more variable locking with a phase-lag which was intermediary between inphase and antiphase. This type of collective behavior is reminiscent of coordination within subjects observed in many studies (see Kelso [39] for review).

Cases with minimal social valence were observed when the relative phase was not deflected by the establishment of the coupling (the slope at which the relative phase drifted remained identical at the onset of the visual contact, see Fig. 2A). This case is described as "social neglect" as it probably requires both subjects to withdraw their attention from their partner's behavior. In contrast, social behaviors were defined when the collective variable was affected at the establishment of visual contact. The consequence was either to repel or to promote coordination. A pattern of behavior which suggested the presence of a coupling despite the failure of synchronization was the drift apart of each oscillator's frequency at the on-set of visual contact (Fig. 2B). For 1:1 coordination modes, such behaviors minimize the likeliness of phaselocking and are probably best regarded as instances of social segregation. However, the very existence of this change at the onset of the visual contact testified that social situation affected the subjects' behavior. Its contrary was social integration, encountered when the frequencies of movements produced by each subjects came closer (71% of the trials). Sometimes, this frequency rapprochement did not allow enough proximity to enable phase-locking (13%) of the trials). Other times, successful social integration was met, by order of increasing strength: (1) when the oscillations showed occasional phase-locking (33% of the trials; see example Fig. 2C), (2) when the oscillations exhibited the quick establishment of phase-locking which was sustained until the cessation of visual contact (25% of the trials; see example Fig. 2D), and finally (3), when this phase-locking was sustained so much as to enable its persistence after the visual contact was removed.

4 Personal brain dynamics of interpersonal behavioral coordination

Following the classification of behavioral patterns, we attempted to identify neuromarkers of coordinated and uncoordinated social behaviors. We analyzed the subjects' EEG in the spectral domain in the range 7.5-13 Hz. The identification of neuromarkers was addressed in two steps: first, stationary trials were used to detect rhythms induced by different behaviors of social integration and segregation. Second, the identified rhythms were inspected to

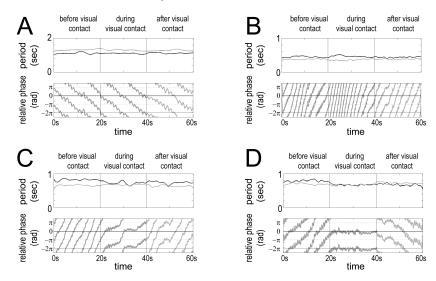


Fig. 2. Representative behaviors of social neglect (A), frequency estrangement (B), transient phase-locking (C) and sustained phase-locking (D). In each case, the upper plot shows the time course of the instantaneous period of movement for each subject and the lower plot shows the relative phase between the two movements. The period of visual contact during which coordination is possible extends from 20 to 40 sec in one minute trials. Social coordination is observed when the frequencies become identical and the relative phase settles.

identify direct brain-behavior relationships, especially during transition from coordination to independent behavior.

Simultaneous acquisition of both subjects' brain activity was achieved with a Dual-EEG system, consisting of two 64-electrode montages from the 10 percent system [12], at the exclusion of rows 9 and 10. Reference electrodes were placed over the linked left and right mastoids of each subject and ground electrodes were located on their forehead at location FPz. Impedances were maintained below 10 k Ω . Data acquisition was performed using a Synamp 2 amplifier (Neuroscan, Texas, El Paso). Signals were analog filtered (Butterworth, bandpass from 0.05 Hz -12 dB/octave- to 200 Hz -24 dB/octave-), amplified (gain = 2010) and digitized at 1000 Hz with a 24 bits vertical resolution in the range 950 μ V (sensitivity of 0.11nV).

Single-trial EEG spectra were estimated in each condition (before, during and after visual contact) within homogenous classes of coordination behavior (complete phase-locking and complete absence of phase-locking). Transients were discarded at the onset and offset of each 20 sec period (3 sec and 0.6 sec respectively). A tukey window (10%) was applied to the remaining data and EEG spectral amplitudes were derived from a Discrete Fourier Transform. These spectra best represent brain activity which is sustained over the entire

window, under the assumption that underlying brain dynamics is stationary, which is met when the behavior itself is stationary.

Due to the large size of the window over which the spectral analysis was performed (16.4 sec, or 16384 points at a sampling rate of 1000 Hz), the resulting spectral resolution (0.06 Hz) was orders of magnitudes higher than classical behavioral and cognitive EEG studies (usually 1 Hz). It allowed precise differentiation of the EEG rhythms in the alpha range. We applied a colorimetric model to the electrode space to visualize the topographical patterning of the rhythms [60] and identified three rhythms in the range 7.5-13 Hz, located respectively above rolandic, occipital and right centroparietal regions.

When visual coupling was established, two prominent changes in classical EEG rhythms occurred: occipital α and rolandic μ rhythms were depressed as compared to baseline (μ isolated in 8 subjects: -20.1%; α isolated in 9 subjects: -30.44%). However, changes in those two rhythms were not differentially affected by the pattern of collective behavior. We identify a third rhythm (which we called ϕ) composed of two adjacent spectral components (ϕ_1 and ϕ_2 , see Fig. 3A) both appearing above right centroparietal electrodes (Fig. 3B) at frequencies of 10-12 Hz. Their boundaries were identified by plotting spectral difference between the left and right hemisphere. This technique emphasizes ϕ by canceling out large symmetrical components, among which μ and α (see Fig. 3A).

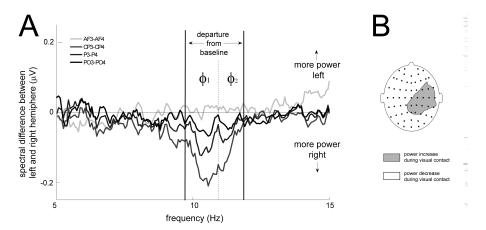


Fig. 3. Spectral (A) and spatial (B) identification of phi complex in a representative subject. (A) The two adjacent component of the phi complex are best seen by plotting the spectral difference between pairs of electrodes in the left and right hemisphere, as the symmetrical rhythms (mu and alpha) cancel out. (B) Representative topographical map in the phi band in a subject. The line shows isopotential (same power before and during visual contact), the area shaded in gray shows selective increase in power attributable to ϕ_1 . ϕ_2 has a similar topography.

Both ϕ components were characterized by power increase during visual contact but they were functionally distinct and their reactivity was mutually exclusive. Increase in ϕ_1 always occurred during uncoordinated trials (identified in 4 subjects: +12.1%; see Fig. 4A). Increase in ϕ_2 always occurred during coordinated trials (identified in 5 subjects: +9.6%) and never occurred during uncoordinated trials (Fig. 4B). We concluded that ϕ_1 promoted intrinsic behavior and ϕ_2 promoted social behavior.

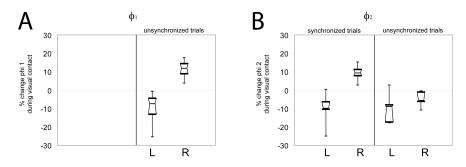


Fig. 4. (A) Box-and-whisker plot of ϕ_1 shows its selective increase in the right hemisphere during unsynchronized trials (ϕ_1 changes during synchronized behaviors not depicted: when ϕ_1 was active in a subject, his/her pair did not produce synchronized behavior). (B) Box-and-whisker plot of ϕ_2 shows its selective increase in the right hemisphere during synchronized trials. (L: left hemisphere - R: right hemisphere).

While the high-resolution spectral analysis provides great details on the spectral band and topography of each rhythm in individual subjects, it is blind to instantaneous changes in brain activity that may accompany behavioral events (see Sec. 2.1). In a second phase, we analyzed the continuous brain dynamics using time-frequency-power plots derived from a Continuous Wavelet Transform (Morlet wavelet). Focusing on the spectral band of ϕ , we attempted to identify its dynamics during trials of sustained or transient coordination. The instantaneous dynamics of ϕ was directly observable in a few subjects, those whose μ and α bore little spectral power (μ and α decrease during visual contact being potentially compensated by the rise of ϕ in subjects presenting notable spectral density in all three rhythms). During stationary trials of coordination, we observed repeated occurrence of very brief, high amplitude bursts in ϕ_2 band (number of bursts typically in the tens during the 20 sec periods, each lasting only 2 or 3 cycles, with an amplitude many fold above the background power in that band). We also identified the disappearance of those bursts during briefs periods of loss of coordinative stability between the subjects' movements (Fig. 5). Such observations may allow for studying instantaneous brain behaviors interactions, a strategy that could be furthered with an adequate decomposition of the spectrum into its respective rhythms so as to generalize the study to all subjects exhibiting ϕ rhythm irrespective of their α and μ 's spectral power.

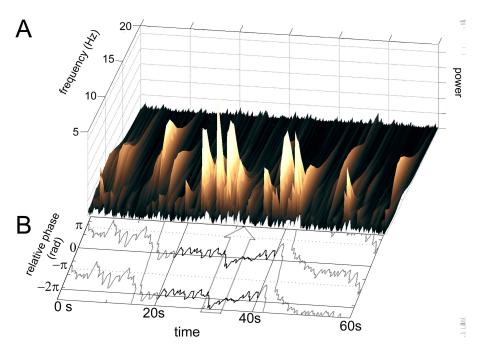


Fig. 5. (A) Time-Frequency-Power plot showing recurrent bursts of ϕ_2 during visual contact (from 20 to 40 sec), with a gap at 32 sec corresponding to a brief lapse of coordinative stability, as seen on the behavioral relative phase (grey arrow in B).

5 Brain dynamics for coordinated and uncoordinated behaviors

While belonging to the field of social neuroscience, the previous results characterized individual brain dynamics. But it remains to characterize coordination between brains. In situations when humans interact, actionperception coupling occurs. It implies dependencies between brain rhythms, which is the next frontier of Social Neuroscience. In social systems composed of several brains, such dependencies follow hard-wired as well as informational paths (Fig. 6). Accordingly, their mechanisms are likely to be found amongst classical large-scale linear coupling [7] as well as other modes of coordination comprising amplitude/amplitude and amplitude/phase spectral correlation, nonlinear coupling between functionally analogous areas of distinct structural and functional characteristics (e.g. the same functional system in different

brains) and non-linear coupling between functionally distinct areas (different functional systems in different brains). Conceptual and empirical efforts to characterize such social brain mechanisms are a foreseeable domain of future research.

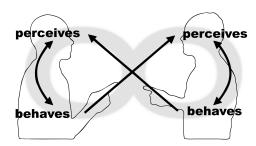


Fig. 6. Action~perception coupling in pairs of individuals. Between-subjects' action~perception is an informational coupling whereas within-brain perception~action is supported by neural connectivity.

In the first decades of the EEG era, electroencephalographers were spending a lot of time scrutinizing their EEG polygraphs and deriving some instantaneous information about brain activity. A very direct approach of brain~behavior causality was then available. With the venue of the digital era, this too qualitative approach went to be replaced with quantitative methods and continuous brain activity got substituted with reconstructed dynamics, especially in the domain of cognitive neuroscience. There, understanding of the brain's instantaneous reactivity to sparse behavioral transitions has been merely lost. We showed that using robust brain responses arising from long known properties of oscillatory entrainment, it was possible to restore a framework of continuous EEG analysis in the prospect of uncovering brain~behavior co-implications.

Applying this framework of EEG Coordination Dynamics to the study of interpersonal coordination, we showed the existence of neuromarkers in the 10 Hz range and presented specimens of instantaneous brain~behavior co-occurrence. ϕ_1 was recruited when subjects maintained a behavior which was distinct from their partners'. ϕ_2 was recruited when subjects adopted coordinated behavior. Both social segregation and social integration are probably adaptive facets of human behaviors. During performance of certain specific tasks, it may be advantageous for subjects to adjust their behaviors. For instance, if a pair of subjects is walking while carrying a load, they may need to adopt the same frequency and to coordinate their pace's "phases". There are also tasks during which social segregation, and not integration, may be adaptive.

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Social integration is further engaged into higher level social behaviors: overt adjustments has been suggested as a mechanism for social facilitation and empathy [5, 50] covert adjustments (stimulation of the motor system by perceived action without associated production of a behavior) for action understanding by direct matching of a conspecific's motor behavior into one's motor system [4, 23, 21] and for skill learning [31]. The implication of ϕ in this range of social processes is an open question.

While the identification of the ϕ complex may help to understand a large range of social behavior in a single brain, there is still one step up for the field of Social Neuroscience to which Coordination Dynamics may contribute. Behavioral contexts exert pressure on individual brains to coordinate, realizing some action~perception coupling at the level of "societies of brains". Models of coordination could be extended to the interpersonal level to describe reciprocal effects of brains on each others when subjects are constrained by a common task.

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