

Toward a Complementary Neuroscience: Metastable Coordination Dynamics of the Brain

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Abstract. Metastability has been proposed as a new principle of behavioral and brain function and may point the way to a truly complementary neuroscience. From elementary coordination dynamics we show explicitly that metastability is a result of a symmetry breaking caused by the subtle interplay of two forces: the tendency of the components to couple together and the tendency of the components to express their intrinsic independent behavior. The metastable regime reconciles the well-known tendencies of specialized brain regions to express their autonomy (segregation) and the tendencies for those regions to work together as a synergy (integration). Integration ~ segregation is just one of the complementary pairs (denoted by the tilde (~) symbol) to emerge from the science of coordination dynamics. We discuss metastability in the brain by describing the favorable conditions existing for its emergence and by deriving some predictions for its empirical characterization in neurophysiological recordings.

Keywords: brain, metastability, the complementary nature, coordination dynamics, consciousness

1 Prolegomenon

This essay starts with some *considerata* for science in general and cognitive computational neuroscience, in particular. It then focuses on a specific, empirically grounded model of behavioral and brain function that emanates from the theoretical framework of coordination dynamics. This model contains a number of attractive properties, one of which, metastability, has been acclaimed as a new principle of brain function. The term metastability is on the rise; it is well-known in physics and has been embraced by a number of well-known neuroscientists. As we explain, it is not the word itself that matters, but rather what the word means for understanding brain and cognitive function. In coordination dynamics, metastability is not a concept or an idea, but a fact that arises as a result of the observed self-organizing nature of both brain and behavior. Specifically, metastability is a result of broken symmetry in the relative phase equation that expresses the coordination between nonlinearly coupled (nonlinear) oscillators. The latter design is motivated by empirical evidence showing that the structural units of the brain which support sensory, motor and cognitive

processes typically express themselves as oscillations with well-defined spectral properties. According to coordination dynamics, nonlinear coupling among heterogeneous components is necessary to generate the broad range of brain behaviors observed, including pattern formation, multistability, switching (sans “switches”), hysteresis and metastability. Metastable coordination dynamics reconciles the well-known tendencies of specialized brain regions to express their autonomy, with the tendencies for those regions to work together as a synergy. We discuss metastability in the brain by describing the favorable conditions existing for its emergence and by deriving some predictions for its empirical characterization in neurophysiological recordings. A brief dialogue follows that clarifies and reconciles the present approach with that of W. Freeman. Finally, we explore briefly some of the implications of metastable coordination dynamics for perception and thinking.

2 Toward a Complementary Science

Up until the time of Bohr, Heisenberg and Pauli, scientists debated over whether light, sound and atomic scale processes were more basically particle-like or wave-like in character. Philosophy spoke of thesis and antithesis, of dialectic tension, of self and not self, of the qualitative and the quantitative, the objective and the subjective, as if they were either/or divisions. This tendency to dichotomize, to divide the world into opposing categories appears to be a ‘built in’ property of human beings, arising very early in development and independent of cultural background [1]. It is, of course, central to the hypothetico-deductive method of modern science which has made tremendous progress by testing alternative hypotheses, moving forward when it rejects alternatives. Or so it seems.

For Bohr, Pauli and Heisenberg, three giants of 20th century science and chief architects of the most successful theory of all time, it became abundantly clear that sharp dichotomies and contrarities must be replaced with far more subtle and sophisticated complementarities. For all of nature, human nature (and presumably human brains) included. Probably Pauli [2] expressed it best:

“To us the only acceptable point of view appears to be one that recognizes both sides of reality—the quantitative and the qualitative, the physical and the psychological—as compatible with each other. It would be most satisfactory of all if physics and psyche could be seen as complementary aspects of the same reality” (p.260).

The remarkable developments of quantum mechanics demonstrating the essential complementarity of both light and matter should have ushered in not just a novel epistemology but a generalized complementary science. However, they did not. Thinking in terms of contraries and the either/or comes naturally to the human mind. Much harder to grasp is the notion that contraries are complementary, *contraria sunt complementa* as Bohr’s famous coat of arms says. One step in this direction might be if complementary aspects and their dynamics were found not just at the level of the

subatomic processes dealt with by quantum mechanics, but at the level of human brains and human behavior dealt with by coordination dynamics.

3 Toward a Complementary Brain Science

How might a complementary stance impact on understanding the brain? The history of brain research over the last few centuries is no stranger to dichotomy: it contains two conflicting theories of how the human brain works (see [3] for an excellent treatment). One theory stresses that the brain consists of a vast collection of distinct regions each localizable in the cerebral cortex and each capable of performing a unique function. The other school of thought looks upon the brain not as a collection of specialized centers, but as a highly integrated organ. In this view, no single function can be the sole domain of any unique part of the cortex. Obeying the old dictum, the holistic brain is greater than and different from the sum of its parts. Like debates on nature versus nurture, learning versus innateness, reductionism versus holism, these two conflicting views of how the brain works have shed more heat than light. Yet surprisingly, the two either-or contrasts still survive. In modern parlance, researchers ask if the brain is “segregated” into its parts or “integrated” as a whole, if information is represented in a modular, category-specific way or in a distributed fashion in which many distinct areas of the brain are engaged, each one representing many different kinds of information.

In the last 20 years or so some new ideas about brain organization have emerged that may provide deeper insight into the human mind, both individual and collective. One step in this direction is by Sungchui Ji [4]. In promoting his “complementarist” epistemology and ontology, Ji draws on the biology of the human brain, namely the complementary nature of its hemispheric specializations. For Ji, the left and right hemispheres have relatively distinct psychological functions and “ultimate reality,” as perceived and communicated by the human brain, is a complementary union of opposites [4]. This is a picture painted with a very broad brush. On a much finer grained scale, Stephen Grossberg [5] in a paper entitled “The Complementary Brain” has drawn attention to the complementary nature of brain processes. For example, the visual system is divided by virtue of its sensitivity to different aspects of the world, form and motion information being carried by ventral and dorsal cortical pathways. For Grossberg, working memory order is complementary to working memory rate, color processing is complementary to luminance processing and so forth. Grossberg believes that the brain is organized this way in order to process complementary types of information in the environment. For him, a goal of future research is to study more directly how complementary aspects of the physical world are translated into complementary brain designs for coping with this world.

If the brain, like the physical world, is indeed organized around principles of complementarity, why then do we persist in partitioning it into contraries? What is it that fragments the world and life itself? Is it the way nature is? Or is it us, the way we are? (see how pernicious the either/or is!). Of course, this age-old question goes back

thousands of years and appears again and again in the history of human thought, right up to the present [6], [7]. Outside quantum mechanics, however, no satisfactory answer from science has emerged. Motivated by new empirical and theoretical developments in coordination dynamics, the science of coordination, Kelso and Engström [7] have offered an answer, namely that the reason the mind fragments the world into dichotomies (and more important how opposing tendencies are reconciled) is deeply connected to the way the human brain works, in particular its *metastable coordination dynamics* (e.g., [8], [9], [10], [11], [12], [13], [14]). Let's summarize some of the general aspects of coordination dynamics, before focusing in on its core mathematical form.

4 Coordination Dynamics of the Brain: Multistability, Phase Transitions and Metastability

From being on the periphery of the neurosciences for fifty years and more, brain dynamics is steadily inching toward center stage. There are at least four reasons for this. One is that techniques at many levels of description now afford an examination of both structure and function in real time: from gene expression to individual neurons to cellular assemblies and on to behavior, structures and their interrelation. Two is that slowly and surely the concepts, methods and tools of self-organizing dynamical systems are taking hold. It is twenty years since a review article in *Science* laid out the reasons why [15]. Three is that dynamics is a language for connecting events from the genetic to the mental [12]. Dynamics is and must be filled with content, each level possessing its own descriptions and quasi-autonomy (everything is linked, from a particle of dust to a star). Four is that empirical evidence indicates that dynamics appear to be profoundly linked to a broad range of disorders ranging from Parkinson's disease to autism and schizophrenia.

The theory of coordination dynamics is based on a good deal of empirical evidence about how brains are coordinated in space and time. One key set of results is that neurons in different parts of the brain oscillate at different frequencies (see [16], [17] for excellent reviews). These oscillations are coupled or "bound" together into a coherent network when people attend to a stimulus, perceive, think and act [18], [19], [20], [21], [22], [23], [24], [25], [26]. This is a dynamic, self-assembling process, parts of the brain engaging and disengaging in time, as in a good old country square dance. Such a coordinative mechanism may allow different perceptual features of an object, different aspects of a moving scene, separate remembered parts of a significant experience, even different ideas that arise in a conversation to be bound together into a coherent entity.

Extending notions in which the 'informational code' lies in the transient coupling of functional units, with physiological significance given to specific phase-lags realized between coordinating elements [27], we propose that phase relationships carry information, with multiple attractors (attracting tendencies) setting alternatives for complementary aspects to emerge in consciousness [28]. In the simplest case,

oscillations in different brain regions can lock “in-phase”, brain activities rising and falling together, or “anti-phase”, one oscillatory brain activity reaching its peak as another hits its trough and vice-versa. In-phase and antiphase are just two out of many possible multistable phase states that can exist between multiple, different, specialized brain areas depending on their respective intrinsic properties, broken symmetry and complex mutual influence.

Not only does the brain possess many different phase relations within and among its many diverse and interconnected parts, but it can also switch flexibly from one phase relation to another (in principle within the same coalition of functional units), causing abrupt changes in perception, attention, memory and action. These switchings are literally “phase transitions” in the brain, abrupt shifts in brain states caused by external and internal influences such as the varying concentration of neuromodulators and neurotransmitter substances in cell bodies and synapses, places where one neuron connects to another.

Coordination dynamics affords the brain the capacity to lock into one of many available stable coordinative states or phase relations. The brain can also become unstable and switch to some completely different coordinative state. Instability, in this view, is a selection mechanism picking out the most suitable brain state for the circumstances at hand. Locking in and switching capabilities can be adaptive and useful, or maladaptive and harmful. They could apply as easily to the schizophrenic or obsessive-compulsive, as they could to the surgeon honing her skills.

A third kind of brain dynamic called metastability is becoming recognized as perhaps the most important of all for understanding ourselves. In this regime there are no longer any stable, phase and frequency synchronized brain states; the individual regions of the brain are no longer fully ‘locked in’ or interdependent. Nor, ironically enough, are they completely independent. According to a recent review [29]:

*“Metastability is an entirely new conception of brain functioning where the individual parts of the brain exhibit tendencies to function autonomously **at the same time (emphasis ours)** as they exhibit tendencies for coordinated activity (Kelso, 1991; 1992; 1995; Bressler & Kelso, 2001; see also Bressler, 2003)”*

As the Fingelkurts’s remark, metastability is an entirely new conception of brain organization, not merely a blend of the old. Individualist tendencies for the diverse regions of the brain to express themselves coexist with coordinative tendencies to couple and cooperate as a whole. In the metastable brain, local and global processes coexist as a complementary pair, not as conflicting theories. Metastability, by reducing the strong hierarchical coupling between the parts of a complex system while allowing them to retain their individuality leads to a looser, more secure, more flexible form of function that can promote the creation of new information. No dictator tells the parts what to do. Too much autonomy of the component parts means no chance of coordinating them together. On the other hand, too much interdependence and the system gets stuck, global flexibility is lost.

Metastability introduces four advantageous characteristics that neurocognitive models are invited to consider. First, metastability accommodates heterogeneous elements (e.g. brain areas having disparate intrinsic dynamics; brain areas whose activity is associated with the movement of body parts or events in the environment). Second, metastability does not require a disengagement mechanism as when the system is in an attractor and has to switch to another state. This can be costly in terms of time, energy and information processing. In the metastable regime, neither stochastic noise nor parameter changes are necessary for the system to explore its patternings. Third, metastability allows the nervous system to flexibly browse through a set of possibilities (tendencies of the system) rather than adopting a single ‘point of view’. Fourth, the metastable brain favors no extremes. Nor is it a “balance” of opposing alternatives. For example, it makes no sense to say the brain is 60% segregated and 40% integrated. Rather, metastability is an expression of the full complexity of the brain.

A number of neuroscientists have embraced metastability as playing a role in various neurocognitive functions, including consciousness (e.g. [14], [25], [30], [31], [32], [33], [34], [35], [36], [37]). As we explain below, it is not the word itself that matters, but what the word means for *understanding*. In coordination dynamics, metastability is not a concept or an idea, but a consequence of the observed self-organizing and pattern forming nature of brain, cognition and behavior [12], [15], [38], [39]. Specifically, metastability is a result of the broken symmetry of a system of (nonlinearly) coupled (nonlinear) oscillators called the *extended HKB model* [40]: *HKB* stands for Haken, Kelso and Bunz [41] and represents a core (idealized) dynamical description of coordinated brain and behavioral activity (see e.g. [42]). Importantly, it is the symmetry breaking property of the extended HKB model [40] that has led to metastability and the new insights it affords.

5 The Extended HKB Model

Etymologically, ‘metastability’, comes from the latin ‘*meta*’ (beyond) and ‘*stabilis*’ (able to stand). In coordination dynamics, metastability corresponds to a regime near a saddle-node or tangent bifurcation in which stable coordination states no longer exist (e.g., in-phase synchronization where the relative phase between oscillating components lingers at zero), but attraction remains to where those fixed points used to be (‘remnants of attractor-repellors’). This gives rise to a dynamical flow consisting of phase trapping and phase scattering. Metastability is thus the simultaneous realization of two competing tendencies: the tendency of the components to couple together and the tendency for the components to express their intrinsic independent behavior. Metastability was first identified in a classical model of coordination dynamics called the extended HKB [40], and later seen as a potential way by which the brain could operate [8], [10], [11], [12], [29], [30], [35], [43], [44].

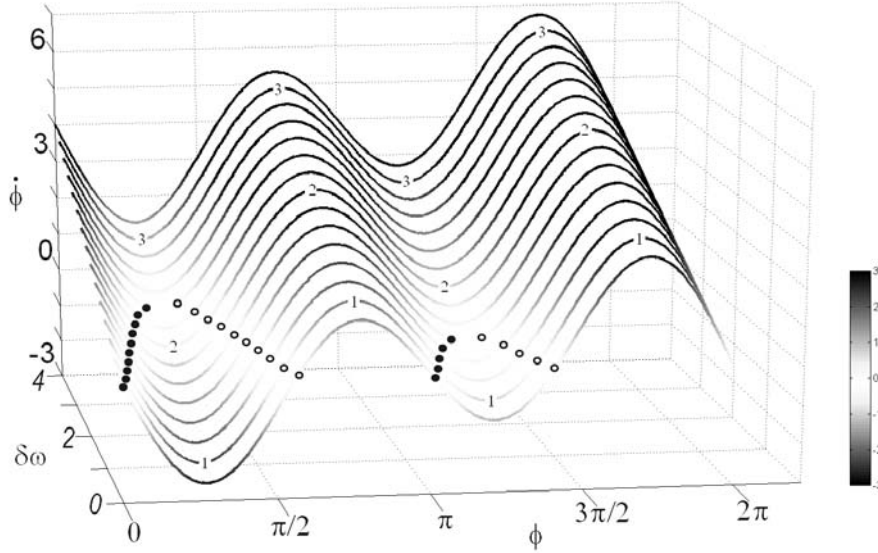


Fig. 1. Surface formed with the flows of the coordination variable ϕ (in radians) for increasing values of $\delta\omega$ between 0 and 4. For this example, the coupling is fixed: $a=1$ and $b=1$. When $\dot{\phi}$ reaches zero (flow line becoming white), the system ceases to change and fixed point behavior is observed. Stable and unstable fixed points at the intersection of the flow lines with the isoplane $\dot{\phi}=0$ are represented as filled and open circles respectively. To illustrate the different regimes of the system, three representative lines labeled 1 to 3 fix $\delta\omega$ at increasing values. Following the flow line 1 from left to right, two stable fixed points (filled circles) and two unstable fixed points (open circles) exist. This flow belongs to the multistable (here bistable) regime. Following line 2 from left to right, one pair of stable and unstable fixed points is met on the left, but notice the complete disappearance of fixed point behavior on the right side of the figure. That is, a qualitative change (bifurcation; phase transition) has occurred. The flow now belongs to the monostable regime. Following line 3 from left to right, no stable or unstable fixed points exist yet coordination has not disappeared. This flow corresponds to the metastable regime, which is a subtle blend of coupling and intrinsic differences between the components.

The equation governing the coordination dynamics of the extended HKB model describes changes of the relative phase over time ($\dot{\phi}$) as:

$$\dot{\phi} = \delta\omega - a \sin \phi - 2b \sin(2\phi) + \sqrt{Q}\xi t . \quad (1)$$

where ϕ is the relative phase between two interacting components, a and b are parameters setting the strength of attracting regions in the system's dynamical landscape, $\sqrt{Q}\xi t$ is a noise term, and $\delta\omega$ is a symmetry breaking term arising from

each component having its own intrinsic behavior. The introduction of this symmetry breaking term $\delta\omega$ (equation 1) changes the entire dynamics (layout of the fixed points, bifurcation structure) of the original HKB system. It is the subtle interplay between the coupling term ($k=b/a$) in equation 1 and the symmetry breaking term, $\delta\omega$, that gives rise to metastability.

The flow of the coordination dynamics across a range of values of $\delta\omega$ is presented in Figure 1 for a fixed value of the coupling parameter, $k = b/a=1$ where $a=1$ and $b=1$). Stable fixed points (attractors) are presented as filled circles and unstable fixed points (repellers) as open circles. Note these fixed points refer to the coordination variable or order parameter: the relative phase (see Section 7 for further discussion of the order parameter concept). A fixed point of the coordination variable ϕ represents a steady phase- and frequency relationship between the oscillatory components or *phase-locking*. The surface shown in Figure 1 defines three regions under the influence of the symmetry breaking term $\delta\omega$. In the first region present in the lower part of the surface, the system is multistable. Following the representative line labeled 1 in Figure 1 from left to right, two stable fixed points (filled circles) are met which are the alternatives for the system to settle in. Which one, depends on the initial conditions and the size of the basin of attraction. In an intermediate region, following the line labeled 2 from left to right, one observes that the weakest attractor near anti-phase (right side) disappears after it collides with its associated repeller somewhere near $\delta\omega=1.3$, but the strongest attractor (left side) is still present as well as its repeller partner. Finally in the third region in the upper part of the surface, the regime becomes metastable. Following the line labeled 3 from left to right, no fixed points exist anymore (this part of the surface no longer intersects the isoplane $\dot{\phi}=0$ where the fixed points are located).

What does coordination behavior look like in the metastable regime? Although all the fixed points have vanished, a key aspect is that there are still some traces of coordination, ‘ghosts’ or ‘remnants’ of where the fixed points once were. These create a unique dynamics alternating between two types of periods which may be called dwell time and escape time. Escape times are observed when the trajectory of the coordination variable, relative phase, drifts or diverges from the horizontal. Dwell times are observed when the trajectory converges and holds (to varying degrees) around the horizontal. In Figure 2c we show two locations for the dwell times: one that lingers a long time before escaping (e.g. Figure 2c, annotation 1) slightly above the more stable in-phase pattern near 0 rad (modulo 2π), and the other that lingers only briefly (e.g. Figure 2c, annotation 2) slightly above π (modulo 2π). The dwell time is reminiscent of the transient inflexions observed near the disappeared attractor-repeller pairs in the monostable regime (Figure 2b, annotation 3). These inflexions recur over and over again as long as the system is maintained in the metastable regime, i.e. as long as it does not undergo a phase transition.

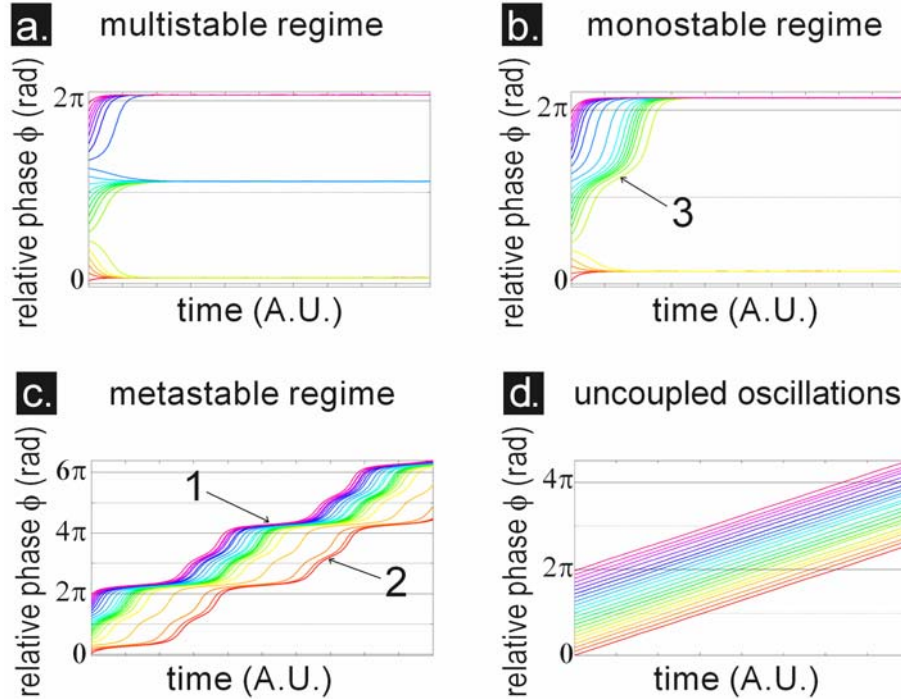


Fig. 2. Examples of trajectories of the coordination variable, relative phase ϕ arising from a range of initial conditions sampled between 0 and 2π radians, in the multistable (a), monostable (b) and metastable regimes (c) of the extended-HKB model. Trajectories in the multistable regime converge either to an attractor located slightly above 0 rad. modulo 2π or to another attractor located slightly above π rad. modulo 2π . In the monostable regime (a), trajectories converge to an attractor located slightly above 0 rad. modulo 2π . In the trajectories of relative phase for the metastable regime (c. unwrapped to convey continuity), there is no longer any persisting convergence to the fixed points, but rather a succession of periods of rapid drift (escape time) interspersed with periods inflecting toward, but not remaining on the horizontal (dwell time). Note dwells nearby 0 rad. modulo 2π in the metastable regime (e.g. dwell time at about 4π rad. annotated 1 in Fig 2c) and nearby π rad. modulo 2π (dwell time at about 3π rad. annotated 2 in c.) are reminiscent of the transient obtained for certain initial conditions in the monostable regime (b. annotation 3). For reference, the relative phase of uncoupled oscillators is displayed in (d.).

Despite the complete absence of phase-locked attractors, the behavior of the elements in the metastable regime is not totally independent. Rather, the dependence between the elements takes the form of dwellings (phase gathering) nearby the remnants of the fixed points and is expressed by concentrations in the histogram of the relative phase (see [12], Chapter 4). Can the brain make use of such a principle? In contrast to, or as a complement of theories of large-scale organization through linear phase-coupling [18], [19], [45], [25], our thesis is that the ability of the system

to coordinate or compute without attractors opens a large set of possibilities. The classical view of phase-locked coordination prescribes that each recruited element loses its intrinsic behavior and obeys the dictates of the assembly. When such situations arise, from the functional point of view, individual areas cease to exert an influence for the duration of the synchronized state, and the pertinent spatial level of description of the unitary activity becomes the synchronous assembly itself. However, phylogenesis promoted specialized activity of local populations of neurons [30], [46], [47], [48], [49]. In theories proposing large-scale integration through phase synchronization, the expression of local activity can only exist when the area is not enslaved into an assembly, whereas in the metastable regime, the tendency for individual activity is more continually preserved (see also [35]).

As exemplified explicitly in the extended HKB model, a delicate balance between integration (coordination between individual areas) and segregation (expression of individual behavior) is achieved in the metastable regime [11], [12]. Excessive segregation does not allow the proper manifestation of cognition as seen for instance in autism and schizophrenia [50], [51], [52], [53], [54], [55]. On the other hand, excessive integration does not appear to be adaptive either. Resting states measured during cognitive idling are characterized by widespread oscillations across large cortical territories [56], [57], [58], [59], [60] that appear to block or inhibit the proper expression of a local area's activity. Furthermore, propagation of synchronous activity leads to epileptic seizures [61], [62], [63], [64], [65] and is ultimately characterized by a total loss of cognition and consciousness once a certain mass of neurons is recruited. In a critical range between complete integration and complete segregation the most favorable situation for cognition is deemed to occur [44], [66], [67]. Studies of interareal connectivity both at the anatomical and functional level ([35], [68], [69], see also [37]) support this view by showing that measures of complexity reach a maximum when the balance between segregative and integrative forces is achieved. Note, however, that such measures are based upon stationarity assumptions whereas metastability in coordination dynamics is a 'stationary transient'. That is, the holding and releasing of the relative phase over time appears to be of a transient nature, but is actually quite stationary

Another interesting feature related to the absence of attractors is the ability of the system to exhibit more than one coordination tendency in the time course of its life. This property is reminiscent of the multistable regime with attractors, with the difference that no transition is required to switch from one state to the other. Evidence of 'multistability' and spontaneous switching in perception and action abounds both at behavioral and brain levels (e. g., [39], [70], [71], [72], [73], [74], [75], [76], [77]). Aside from the multistable regime with attractors undergoing phase transition, the metastable regime is also suitable to explain those experimental results. The tendencies of the metastable regime toward the remnants of the fixed points readily implements spontaneous reversals of percepts and behaviors described in these studies [78]. From the perspective of coordination dynamics, the time the system dwells in each remnant depends on a subtle blend of the asymmetry of the components (longer dwelling for smaller asymmetry) and the strength of the coupling (longer dwelling for larger values of a or b). Such a mechanism provides a powerful

means to instantiate alternating thoughts/percepts and their probability in both biological systems and their artificial models (e.g. alternating percepts of vase or faces in ambiguous Rubin figures, or alternative choices in the solving of a chess game).

Both a multistable regime with attractors and a metastable regime with attracting tendencies allow so-called perceptual and behavioral ‘multistability’. Which attractor is reached in the multistable regime primarily depends on initial conditions. Once the system is settled into an attractor, a certain amount of noise or a perturbation is required to achieve a switching to another attractor. Or, if control parameters such as attention are modified, a bifurcation or phase transition may occur, meaning an attractor loses stability as the regime changes from multistable to monostable or vice-versa (see Ditzinger & Haken, [79]; [80] for excellent example of such modeling). In the metastable regime, successive visits to the remnants of the fixed points are intrinsic to the time course of the system, and do not require any external source of input. This is an important difference between multistability and metastability and likely translates into an advantage in speed which is known to be an important constraint in neurocognitive systems [81] and a crucial aspect of their performance [82].

6 Metastability in the Brain

What is the anatomical basis in the brain for metastable coordination dynamics? As noted earlier, the fundamental requirements for metastability are the existence of coupled components each exhibiting spontaneous oscillatory behavior and the presence of broken symmetry. There are several spatial scales at which the collective behavior of the brain spontaneously expresses periodic oscillations [83], [84], [85], [86], [87] and represents the combined contribution of groups of neurons, the joint action of which is adequate to establish transfer of information [88], [89], [90]. The oscillatory activity of the brain may be captured directly via invasive neurophysiological methods such as LFP and iEEG, or indirectly from EEG scalp recordings (commonly at the price of estimating local oscillations by bandpass filtering of the signals). The coupling between local groups of neurons is supported by long-range functional connectivity [25], [91], [92]. Broken symmetry has several grounds to spring from, including the incommensurate characteristic frequencies of local populations of neurons [93] and their heterogeneous connectivity [94].

If the conditions required for metastable coordination in the brain are easily met, it remains to establish that the brain actually shows instances of operating in this regime. This empirical characterization encounters some difficulties. Before any attempt to find signatures of metastability, a first question is to identify from the continuous stream of brain activity some segments corresponding to individual regimes. In other words, it consists in finding the transitions between regimes, a task undertaken by only a few [95], [96]. Provided adequate measurement/estimation of local oscillations in the presence of noise and spatial smearing is possible, insights

can be gained by identifying episodes of phase-locking (these forming states) and ascribing their interim periods as transitions (e.g. [25]). In the absence of ad hoc segmentation of the EEG, it remains as a possibility to use behavioral indices as cues to when brain transitions occur (e.g. [39], [73]). The case of metastability is evidently more difficult since the regime is stationary but not stable. Initial attempts have targeted the more recognizable dwell time as a quasi phase-locked event ([29]). To gain understanding on the mechanism, it seems necessary to elaborate strategies that comprise the coordination pattern of the metastable regime in its entirety (dwell and escape time as an inseparable whole) and to establish criteria for the differentiation of state transitions and dwell ~ escape regimes.

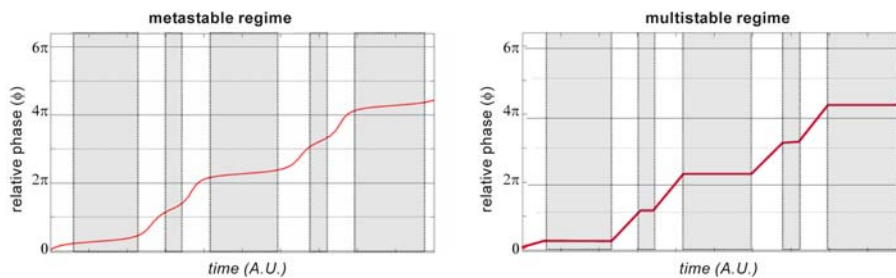


Fig. 3. Comparison of relative phase trajectories in the metastable and multistable regime for a temporal window of arbitrary size. Coordination (multistable regime) and tendency to coordinate (metastable regime) are shown in grey boxes. In the multistable regime (right), a succession of states (stable relative phase near 0 and π radians) is interweaved with transitions. Horizontal segments are lost in the metastable regime (left) which only shows tendencies for synchronization toward inphase and antiphase. In a situation in which coordination is estimated from a broadband signal in the presence of noise, distinguishing between the two regimes may difficult. The transitions on the right however are induced by parametric change; the flow on the left is not.

To identify and understand potential mechanisms, it is of prime importance to be able to distinguish between the different regimes. For instance, a transition between the metastable and the monostable regime could be a way the brain instantiates a process of decision among a set of possibilities. This amounts to the creation of information [97]. Figure 3 shows the isomorphism of simulated systems belonging to both regimes in their relative phases' trajectory. In this window of arbitrary size, a succession of states is shown in the multistable regime (right) separated by transitions. It differs from the metastable regime (left) by the presence of horizontal segments (stable relative phase) during the states and by sharp inflections of the relative phase at the onset and offset of transitions. The corresponding histograms of the relative phase cumulated over this period of time are similar as well. The ability to distinguish the multistable regime from the metastable regime in a non-segmented EEG depends critically on the precision of the estimation of the components' frequency and phase. Unfavorable circumstances are met since the EEG is a noisy, broadband signal [98], and because each component's frequency shifts when coupled in a metastable regime.

Other criteria might be sought for to distinguish between those regimes. State-transition regimes have been conceptually formulated and empirically verified by a line of studies initiated by Eckhorn et al. [18], Gray, Singer et al. [19]. The theory of ‘transient cell assemblies’ has gathered numerous empirical findings at the microscale [99], [100], mesoscale [91], [101], [102] and macroscale [71], [103], [104], [105]. This set of studies relies on linear pairwise phase synchronization methods applied both to Single- and Multi-Unit Activity and Field Potentials. Whereas many studies have focused on the ‘state’ part of the state transition, an interesting feature is seen in the study by Rodriguez et al. [105] of coherent oscillations elicited by Mooney faces. Two periods of intense synchronization at 250 msec and 700 msec are separated by a period of intense desynchronization that the authors described as phase scattering. They suggest that phase scattering is a mechanism by which the brain realizes the transition from a coherent assembly to another assembly--both belonging to stable regimes. Such a mechanism is unnecessary in the succession of tendencies that are characteristic of metastable coordination dynamics.

In summary, the brain by virtue of its properties forms a suitable ground for metastability to take place. The characterization of metastable onsets however is a matter which will certainly require some methodological developments outside the linear approach of transient phase synchronization. In the meantime, indices of metastability are found in the distribution of dwell times near phase-locked states.

7 Clarifying Nonlinear Brain Dynamics: The Freeman-Kelso Dialogue*

Recently, the eminent neurophysiologist Walter Freeman published an article entitled “Metastability, instability and state transitions in neocortex” [34] that led to a discussion with the authors which we think may be useful for clarificatory purposes and to expand awareness of nonlinear brain dynamics. Here we highlight some of the main issues—FAQ about metastable neurodynamics, if you like--in part as a tribute to Freeman and his pioneering work and its relation to coordination dynamics..

First the concept itself. Freeman draws heavily from the solid state physics literature where he notes the concept of metastability has been in use for over 30 years. Although this is correct and many useful analogies have been made between brains and other kinds of cooperative phenomena in nature (e.g., [12], [38], [41], [106], [107]) notice here that metastability arises because of a specific symmetry breaking in the coordination dynamics. That is, intrinsic differences in oscillatory frequency between the components are sufficiently large that they do their own thing, while still retaining a tendency to coordinate together. Thus, the relative phase between the components drifts over time, but is occasionally trapped near remnants of the (idealized) coordinated states e.g., near 0 and π radians (cf. Figure 2). As a consequence of broken symmetry in its coordination dynamics, both brain and

* With the blessing of Walter Freeman

behavior are able to exhibit a far more variable, plastic and fluid form of coordination in which tendencies for the components to function in an independent, segregated fashion coexist with tendencies for the system to behave in an integrated, coordinative fashion.

Second, Freeman inquires about the order parameter in coordination dynamics. Freeman himself pursues spatial patterns of amplitude which he understands as manifestations of new attractors that form through learning. It is these amplitude patterns of aperiodic carrier waves derived from high density EEG recordings that constitute his order parameter. Freeman regards these as evidence for cortical dynamics accessing nonconvergent attractors for brief time periods by state transitions that recur at rates in the theta range. Although we originally also used the physicist's terminology of order parameters (e.g. [39], [41]) we now prefer the term "collective variable" or "coordination variable" as a quantity that characterizes the cooperative behavior of a system with very many microscopic degrees of freedom. Indeed, our approach is called coordination dynamics because it deals fundamentally with informationally meaningful quantities [28]. Coordination in living things is not (or not only) matter in motion. The spatiotemporal ordering observed is functional and task-specific. Because in our studies the variable that changes qualitatively under parametric change is the relative phase, relative phase is one of the key order parameters of biological coordination. Relative phase is the outcome of a nonlinear interaction among nonlinear oscillatory components, yet in turn reciprocally conditions or "orders" the behavior of those components. In a system in which potentially many things can be measured, the variable that changes qualitatively is the one that captures the spatiotemporal ordering among the components. This strategy of identifying order parameters or coordination variables in experimental data goes back to Kelso [74], [75] and the early theoretical modeling by Haken, Kelso & Bunz, [41]. Recent empirical and theoretical research confirms Freeman's work in that it shows that phase transitions can also arise through the amplitudes of oscillation [108]. Both routes are possible depending on the situation, e.g. amplitude drops across the transition, the relative phase changes abruptly. Again, this is all under parametric control. In coordination dynamics, you don't "know" you have a coordination variable or order parameter and control parameters unless the former change qualitatively at transitions, and the latter--when systematically varied--lead the system through transitions. Order parameters and control parameters in the framework of coordination dynamics are thus co-implicative and complementary. An issue in the olfactory system concerns what the control parameters are, e.g. that might lead the system from a steady state to a limit cycle or to chaotic oscillations and itineracy. Both Freeman's and our approach appeal to Haken's [106] synergetics and so-called 'circular' or 'reciprocal causality': whether one adopts the term order parameters or coordination variables, both arise from the cooperation of millions of neurons and in turn are influenced by the very field of activity they create (see also [42], [109] for an elaboration and application of neural field theory).

Two coupled neural ensemble rhythms with noise

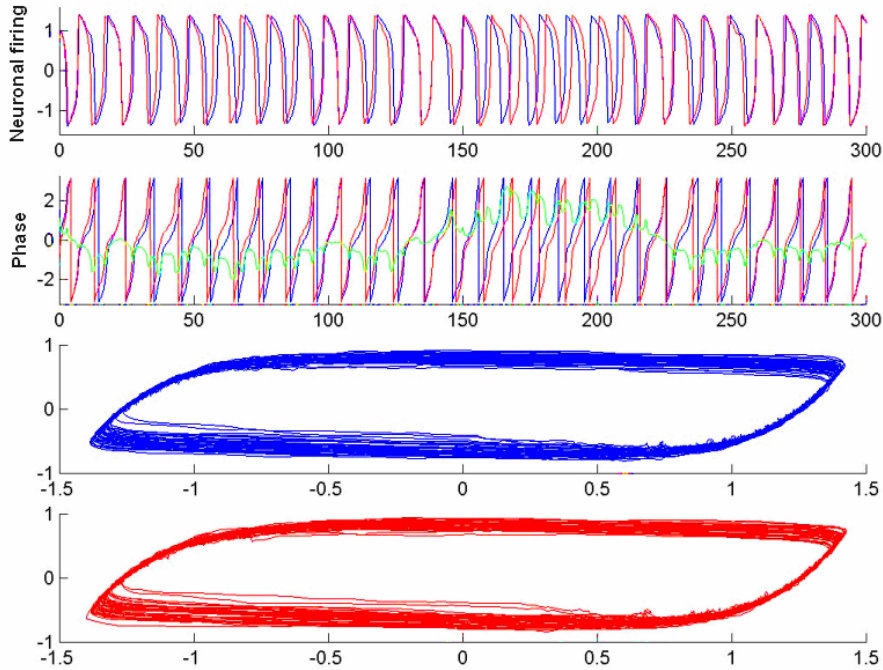


Fig. 4. A simulation of two coupled neural ensembles composed of an array of Fitzhugh-Nagumo oscillators (courtesy Viktor Jirsa). See text for description.

$$\begin{aligned} \frac{dX}{dt} &= F(X) = \frac{\partial}{\partial t} S(X - Y) + noise \\ \frac{dY}{dt} &= F(Y) = \frac{\partial}{\partial t} S(Y - X) + noise \end{aligned} \quad (2)$$

Both Freeman's approach and coordination dynamics appeal to nonlinear coupling among neural oscillators as the basis for varying degrees of global integration. Both make significant use of basin attractor dynamics to interpret experimental data. In coordination dynamics, the latter constitutes a step of idealization that is necessary in order to understand what it means to break the symmetry of the coordination dynamics [40], [97], [110]. Both approaches nevertheless invoke symmetry breaking, coordination dynamics from the loss of attractors of the relative phase dynamics, and Freeman in the emergence of spatial patterns of amplitude and phase from EEG recordings by convergence to a selected *a posteriori* attractor in a landscape of *a priori* attractors. There are obvious parallels between the two bodies of work; both are testament to the richness of detail and power of nonlinear theory. Freeman envisages transient but definite access to a succession of basins of attraction. Metastable

coordination dynamics, on the other hand, has a very precise meaning: it is not about states but a subtle blend of integrative and segregative *tendencies*. Notably, these integrative tendencies to phase gather and segregative tendencies to phase wrap can be shown at the level of coupled neural ensembles. Figure 4 illustrates a set of coupled neural ensembles each composed of one hundred Fitzhugh-Nagumo oscillators connected by a sigmoidal function which is the usual consequence of the summation of threshold properties at cell bodies (equation 2). A small amount of random noise has been added only for illustrative effect. Looking from top to bottom, the neuronal firing activity of each ensemble (X,Y) is shown, followed by the individual oscillatory phases, their relative phase and respective phase plane trajectories indicating limit cycle properties, along with a simple mathematical representation.

The intent here is only to establish proof of concept. It is quite clear that the relative phase between the neural groups dwells near $\phi = 0$, wanders and then returns, indicating nicely the transient metastable tendencies to integrate and segregate. As Fingelkurts and Fingelkurts [29] note:

"One may note that the metastability principle extends the Haken synergetics rules.....Metastability extends them to situations where there are neither stable nor unstable states, only coexisting tendencies (see (Kelso, 2002))"

8 A Short Afterthought

It has not escaped our attention that the metastable coordination dynamics of brain and behavior invites extension to the processes of thought and thinking. A case can be made that multistable perception and ambiguity offer test fields for understanding the self-organization of the brain. The perceptual system, when faced with a constant stimulus, may fluctuate between two or more interpretations. Through ambiguities, as Richard Gregory [111] remarks, we can investigate how the brain makes up its mind. One may speculate that when a naïve perceiver views a figure such as the hidden Dalmatian (Figure 5), a series of mental phases and their associated brain states takes place. In a first stage, the naïve observer may attempt to group the blackened areas in various ways. There will be multistability and phase transitions. Eventually, he/she will correctly organize the picture and a monostable state will be reached in which the Dalmatian's picture is salient. Finally, the observer may think of the artist's work and consider simultaneously the fragmentation that allows the Dalmatian to disintegrate into the scene as well as the organization that hints its presence. A metastable dynamic will arise in which both the figure and its hiding texture will simultaneously be present in the mind. As Heisenberg noted fifty years ago [112]:

"We realize that the situation of complementarity is not confined to the atomic world alone; we meet it when we reflect about a decision and the motives for our decision or when we have a choice between enjoying music and analyzing its structure" (p. 179)



Fig. 5. The hidden Dalmatian

Of course, Heisenberg, Bohr and Pauli's philosophy came from considerations in quantum mechanics. Here both the philosophy of the complementary nature and a complementary neuroscience are rooted in the metastable coordination dynamics of the brain.

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