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Coordination Dynamics

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Article Outline

Glossary

Coordination dynamics Coordination Dynamics, defined broadly as the science of coordination, describes, explains and predicts how patterns of coordination form, adapt, persist and change in living things. In coordination dynamics the parts communicate via mutual information exchange and information is meaningful and specific to the forms coordination takes. Coordination dynamics embraces both spontaneous self-organizing tendencies and the need to guide or direct them in specific ways in a single conceptual framework. Life, brain, mind and behavior are hypothesized to be linked by virtue of sharing a common underlying coordination dynamics.

Synergies Synergies (*aka* coordinative structures) are functional groupings of structural elements (e. g. neurons, muscles, joints) that are temporarily constrained to act as a single coherent unit. They arise in many contexts on many levels of biological organization, from the genetic to the social. Synergies are the key to understanding biological coordination and as such are the significant units of coordination dynamics. The synergy hypothesis is an hypothesis about how Nature handles biological complexity.

Self-organization The 'self' in the word self-organization refers to the ability of an open system that exchanges matter, energy and information with the environment, to organize itself. Spontaneous patterns arise solely as a result of the dynamics of the system with no specific ordering influence imposed from the outside and no

homunculus-like agent inside. Nonequilibrium phase transitions are the hallmark of self-organization in living things.

Collective variables Collective variables (*aka order parameters* in physics or *coordination variables* in coordination dynamics) are relational quantities that are created by the cooperation among the individual parts of a system. Yet they, in turn, govern the behavior of the individual parts. This is sometimes referred to as *circular* or *reciprocal causality*. In coordination dynamics, the identification of coordination variables depends on the level of description. What is "macro" at one level may be "meso" or "micro" at another.

Control parameters Control parameters refer to naturally occurring environmental conditions or intrinsic, endogenous factors that move the system through its repertoire of patterns and cause them to change. Experimentally, you only know for certain you have identified a control parameter if, when varied, it causes the system's behavior to change qualitatively or discontinuously, i. e., to change its functional state.

Metastability Metastability arises due to broken symmetry in the coordination dynamics where the unstable and stable fixed points (phase- and frequency-locked states) have disappeared due to tangent or saddle-node bifurcations leaving behind only remnants of the fixed points. Metastability is the simultaneous realization of two competing tendencies: the tendency of the components to couple together and the tendency of the components to express their intrinsic independent behavior. Metastability has been hailed as a new principle of organization in complex living systems, including the brain, reconciling apparent contraries such as individual and collective, part and whole, competition and cooperation, integration and segregation, and so forth.

Definition of the Subject

Even before man speculated about the nature and sources of his own experiences, he was probably curious about the agencies by which animal motion was affected. Life and motion are almost synonymous terms. Franklin Fearing [48]

In his preface to the *Principia*, Isaac Newton speculated that not just the motions of the planets, the Moon and the tides could be explained by the forces of attraction and repulsion, but all other natural phenomena as well. Despite the hubris, "self-motion", Newton recognized, "was beyond our understanding" [64]. Three and a half centuries later, the problem remains: the goal-directed coordinated movements of animals are not mere mechan-

ical consequences of the laws of physics, at least as we know them. Despite the many remarkable applications of physics to biology and entire fields devoted to them (e. g. biomechanics, biophysics, nanophysics, etc.) and despite the successes of modern molecular biology, the great unresolved problem of biology remains: *how complex living things are coordinated in space and time*. To recognize that coordination is often purposeful and goal-directed does not at all mean a return to vitalism. But it does pose the scientific challenge of extending physics to understand coordination in living things. Coordination dynamics is a response to this challenge: it is a conceptual framework and research program that deals fundamentally with *animate* (and animated) self-organizing dynamical systems (see also [181,182]). That is, it deals with animate organisms anchored to and engaged in their surrounding worlds. Table 1 compares some of the features of classical mechanics and coordination dynamics. The Table is not intended to be inclusive or to convey the idea that there have been no candidate "paradigms" between classical mechanics and coordination dynamics. For present purposes, "the complex systems" paradigm may represent the most recent break from or extension of classical mechanics. In the complex systems paradigm, self-organization would replace organization, open systems would replace closed systems, change, disorder and process would replace stasis, order and equilibrium, etc. [163]. Coordination dynamics goes a step further. In coordination dynamics it is not organization versus self-organization, order versus disorder, closed versus open systems, reductionism versus emergentism, etc., but rather both aspects that are necessary for an exhaustive account of phenomena and a deeper understanding of coordination in living things. Hence, rather than view these features in opposition, they are better viewed as complementary [100,104,110].

Coordination represents one of the most striking, most taken for granted, yet least understood features of all living things. Imagine a living system whose component parts and processes, on any level of description one choose to examine, did not interact with each other or with their surrounds. Such a collective "cell," "organ," "organism" or "society" would possess neither structure nor function. Coordination can be seen almost everywhere we look, whether in the regulatory interactions among genes that affect how an organism develops and how some diseases like cancer occur, the tumbling and twisting of the bacterial flagellum, the coordinated responses of organisms to constantly varying environmental stimuli, the coordination among nerve cells that produce basic forms of locomotion in vertebrates and invertebrates, the coordination among cell assemblies of the brain that underlies our

Coordination Dynamics, Table 1
Some complementary features of classical mechanics and coordination dynamics

Classical Mechanics	Coordination Dynamics
machines; organized	"organisms"; self-organized
inanimate	animate
motion	coordination (function); animation
matter	materially instantiated; organization
forces	information (semantic) and information exchange; couplings
fundamental dimensions (M, L, T)	collective or coordination variables
space, time	spatiotemporal
linear; smooth dynamics	essentially nonlinear; bifurcations; multi- and metastable
deterministic	fluctuations/variability play key role
decomposable;	"emergent"; synergistic;
motion of whole = sum of motion of the parts	motion of whole > sum of motion of the parts
homogeneous parts, elements, components	heterogeneous units and connectivity
micro versus macro level distinction	level independent strategy; 'one level down'
fixed laws	extensible laws; regularities
context-free	context-dependent
machine/artifactual perspective on order	organic/natural perspective on order

awareness, ability to think, remember, decide and act, the miraculous coordination between the lungs, larynx, lips and tongue that belies a child's first word, the learned co-ordination among fingers and brain that allows the skilled pianist to play a concerto, the congruence of motion and emotion in dance, drama and everyday life, the coordination between people – like rowers in a racing eight – working together to achieve a common goal. Everything is co-ordinated.

What do we mean by the word coordination? Coordination is not only spatial and temporal order. Rather, it refers to different kinds and degrees of *functional* or-der among interacting parts and processes in space and time. Newtonian mechanics may define limits on how bi-ological systems are coordinated, but it says nothing about their functional organization, per se. *How are complex living things coordinated in space and time? What is the na-ture of the basic interactions that give rise to patterns of co-ordinated behavior? Why do they take the form they do?* These questions lie at the heart of understanding coordi-nation. Given the ubiquity of coordinated behavior in liv-ing things, one might have expected its lawful basis to have been uncovered many years ago. However, it is only in the last 25 years or so, and under quite peculiar circumstances, that basic laws for a quantitative description of coordina-tion have been found.

Introduction

A centipede was happy quite,
Until a frog in fun said:

"Pray tell which leg comes after which?"
This raised her mind to such a pitch,
She lay distracted in the ditch,
Considering how to run.   Anon

Coordination Dynamics – the science of coordination – refers to the concepts, methods and tools used to describe, explain and predict how patterns of coordination form, adapt, persist, and change in living things. It is about identifying coordinated patterns in the behavior of liv-ing things and expressing how these patterns evolve and change in terms of dynamical laws or rules. The dynam-ics here refers to equations of motion for key *coordination variables* or *order parameters* [73] that characterize coor-dinated patterns of behavior on multiple levels of descrip-tion. As the name implies, the dynamics deals with coordi-nation, not (or not only) with matter in motion: *coordina-tion dynamics* (see Table 1). Through an intimate relation-ship between theory, experiment, analysis and modeling, Coordination Dynamics seeks to identify the laws, prin-ciples and mechanisms underlying coordinated behavior within and between different levels of organization, ex-plicitly addressing the connection between levels. Thus, a goal of Coordination Dynamics is to identify the na-ture of the functional and context-dependent coordina-tion *within* a part of a system (e. g., the firing of cells in the heart or neurons in a part of the brain), *between* dif-ferent parts of a system (e. g., parts of the brain, parts of the body, members of an audience) and *between* dif-ferent kinds of system (e. g., stimuli and responses, or-ganisms and environments, humans and robots, etc.). In

coordination dynamics, the coupling between things is realized by many mechanisms, but is fundamentally informational in nature. That is, Coordination dynamics deals specifically with *meaningfully* coupled, self-organizing systems: the parts communicate via mutual information exchange and information is meaningful and specific to the forms coordination takes. As a source of biological order and pattern, self-organization has received much less attention than the teleonomic, directed nature of living things captured by terms like "program", "blueprint", "template" and so forth. Instead of treating them as opposing theories, Coordination Dynamics unites the spontaneous, self-organizing nature of coordination and the obviously directed, agent-like properties characteristic of animate nature into a single framework [100,104,110]. It does this by studying how functionally meaningful information arises from spontaneous self-organizing processes and how it in turn modifies, guides and directs them.

Coordination Dynamics is both multi- and interdisciplinary, engaging relevant aspects and subfields of psychology, philosophy, biology, neuroscience, computer science, engineering, mathematics and physics. For Coordination Dynamics, a complete understanding of coordination phenomena on *any* given level of description requires: i) specifying the individual coordinating elements and their properties; ii) identifying key parameters, boundary and task conditions that constrain coordination; and (iii) showing how interactions among coordinating elements produce or generate patterns of coordination. By demonstrating in specific cases how the nonlinear coupling among the parts produces coordinated behavior Coordination Dynamics demystifies the popular term "emergence". Even more subtly, a certain régime of Coordination Dynamics called *metastability* resolves the longstanding dichotomy between the whole and the parts by explicitly showing how the individual parts of the system may retain a certain degree of autonomy while still coordinating as a whole. To the extent that they transcend the particular mechanisms through which coordination is realized, the principles of Coordination Dynamics may be said to be "universal" and hence have the potential to describe and explain coordinated behavior in a number of fields ([75]; see also ▶ Movement Coordination and ▶ Social Coordination, from the Perspective of Coordination Dynamics). In the case of movement coordination, for example, Coordination Dynamics provides the basic laws for a quantitative description of phenomena that are observed when humans interact in a certain way with themselves, with other humans and with their environment [59,100].

History of Coordination Dynamics: Synergy and Rhythmic Order

Coordination Dynamics arose as a response to the fundamental problem of control and coordination in complex, biological systems: the problem of degrees of freedom. Consider an ordinary movement of the human body. The body itself consists of over 790 muscles and 100 joints that have co-evolved in a complex environment with a nervous system that contains $\sim 10^{12}$ neurons and neuronal connections. On the sensory side, billions of receptor elements embedded in skin, joints and muscles inform the mover about his movement. Clearly, any ordinary human activity requires the cooperation among very many structurally diverse elements – a miracle that we take for granted (e. g. [164]). How does nature compress the very high dimensional state space of such a complex system into something lower dimensional and controllable? An attractive hypothesis proposed by the Russian physiologist Bernstein (1896–1966 [17]) is that in complex living systems, the individual elements are not controlled directly but are rather organized into collectives called *synergies*. Synergies are functional groupings of structural elements (e. g. neurons, muscles, joints) that are temporarily constrained to act as a single coherent unit. Just as new states of matter form under certain conditions when a group of atoms behaves as a single particle (e. g., the Bose–Einstein condensate) so a new state of biological *function* emerges when large ensembles of different elements form a synergy. The synergy hypothesis is therefore an hypothesis about how Nature handles biological complexity. Synergies may appear in many contexts on many levels of biological organization, from the genetic to the social. Depending on context, synergies can accomplish different functions using some of the same anatomical components (e. g., those used for speaking and chewing) and the same function using different components (e. g. writing one's name with a pen attached to the big toe). Once assembled, the degrees of freedom composing a synergy take care of themselves in a relatively autonomous organization. The assembling and disassembling of synergies may be said to be "soft" demanding little energy: synergies are ready to become something else at an instant. They are the "atoms", the significant units of biological function [105,107].

The hallmark of a synergy is that the individual elements adjust to mutual fluctuations and to fluctuations in the external force field (and more generally, the synergy's environment) in order to sustain integrity of function. As a consequence, natural variations (which from the scientist's view may be seen as "errors") that occur in the individual elements of the synergy are compensated by adjust-

ments ("covariations") in other members of the synergy in such a way as to maintain a given function stable. Retaining stability is, for a synergy, the retaining of functional integrity [105,204]. Stability, therefore, plays a key role in coordination dynamics, where the great challenge is to discover what the stability is of. Since the key variables of coordination are not known a priori in living things, they must be identified through empirical research. This, as we shall see, follows a particular strategy.

In the late 1970s and early 80s technological developments and sophisticated computer methods for analyzing complex, multidegree of freedom movements enabled stringent experimental tests of the synergy hypothesis to be carried out [112,120]. Invariably, the experiments, which ranged from postural control to speech production and complex finger and limb movements ([105,107,136,201,204] for reviews), showed: a) that a perturbation to any part of the putative synergy is rapidly compensated for by remotely linked elements in such a way as to preserve system function; b) that the same elements are used in different functions in different ways; c) that different elements may accomplish the same function; and d) that the adjustments observed could in all cases be said to be meaningful, task- and context-specific. All this evidence for the existence of synergies attests to the tremendous redundancy or degeneracy of biological systems [46].

All scientific journeys begin with a single step. The identification of synergies as significant structural–functional units of biological coordination was an important one for the development of Coordination Dynamics. Synergies simplify control by reducing the number of variables that must be independently specified: as constraints, they make control and coordination of complex, multivariable systems possible. But understanding goes far beyond identification. How are synergies formed? What principles govern their assembly? And how does one synergy change spontaneously to another as internal or external conditions change? How can distinct synergies co-exist among the same set of components? And how are individual components of the synergy engaged and disengaged as circumstances change?

Insights into these questions come from the work of a largely unheralded genius called Erich von Holst [215], a behavioral physiologist who spent his life studying coordination in a wide variety of creatures – from worms to man. Von Holst's research will not give us answers to all the questions about synergies but it will provide key insights into the essence of coordination and a stepping stone to finding the underlying principles. Using an experimental model system that allowed him to measure an ele-

mentary synergy – the to and fro motions of the fins of the swimming dogfish *Labrus* under carefully controlled water flow conditions – von Holst identified at least three basic types of coordination: *absolute* coordination, in which component parts are locked together in time (like the synchronized flashing of fireflies, a couple making love or phase synchrony between parts of the brain); partial or *relative* coordination, in which the component parts 'lock in' only transiently and then break apart as circumstances change (like a little boy walking hand in hand with his father on the beach; dad must slow down and/or son add a step so that they can stay together); and no coordination at all, in which the component parts behave quite independently (as occurs in the locomotion of millipedes and centipedes when the same little boy chops off their middle legs, or perhaps after persistent, long term practice in playing the piano or the violin). Various blends, mixes and transitions between these coordinated behaviors were also observed – always matching the exigencies of the internal and external environment.

Why might some kind of common principle exist for such diverse phenomena? The reason is that the same basic coordination phenomena seem to cut across a wide range of levels, creatures and functions. Among those observed are: patterns of coordination remain stable in time despite continuous, and often unexpected perturbations; the ease with which component parts and processes are flexibly engaged and disengaged as functional demands or environmental conditions change; the existence of multiple coordination patterns – so-called multifunctionality – that effectively satisfy the same set of circumstances; the selection of particular coordination patterns that are exquisitely tailored to suit the current needs of the organism; adaptation of coordination to changing internal and external contingencies; smooth and abrupt transitions from one coordinated pattern to another; transitions from partially to fully coordinated patterns and vice-versa; persistence of a coordinated pattern even when conditions that led to the establishment of the pattern have changed (a kind of memory), and so forth. Such phenomena appear so commonly and so consistently as to suggest the existence of an underlying lawfulness or regularity that transcends the differences between systems. Nature, as the saying goes, operates with ancient themes. Or maybe nature just is what it is.

Conceptual Foundations of Coordination Dynamics: Self-organizing Dynamical Systems

Given we accept the empirical facts about synergies and rhythmic order in the nervous system and the movements of living things, what concepts, methods and tools do we

use to understand them? Were synergies simply rigid mechanical entities built by an engineer or an intelligent designer, control theory with its programs, reference levels, comparators, feedforward and feedback error correcting mechanisms and so forth, might have seemed an obvious place to look for explanatory tools. A program instructs the parts of a system what to do and when to do it. Feedback may then be used to correct errors in the outcome. But now what? The system receives an error signal: How does it know which of its many parts to correct? In a complex system composed of very many components it may take a very long time to come up with a solution, a problem computer scientists refer to as an NP-complete problem, where NP means "non-deterministic polynomial time complete". Biology with its degeneracy and redundancy has no such problem. "Error" signals from one part of a synergy are rapidly compensated by other members. So if anything, the *machine perspective* on order and regulation (Table 1) seems to compound the problem rather than solve it.

Coordination Dynamics takes its inspiration from *a natural, organic perspective*, i. e., how nature handles complexity (Table 1). It is well-known that pattern formation in open, nonequilibrium physical and chemical systems such as fluids, lasers and chemical reactions can emerge spontaneously. These patterns arise solely as a result of the dynamics of the system with no specific ordering influence imposed from the outside environment and no homunculus-like agent inside. Such "self-organized" pattern formation is a cooperative phenomenon that results from the interaction of large numbers of interacting subsystems [73,152]. It should be stressed here that there is no "self" inside the system responsible for prescribing or coding the emergent pattern. The 'self' in self-organization comes from the fact that given the ability to exchange matter, energy and information with the environment, the system organizes itself. That the organism is an open system is one of two essential criteria for life postulated by Francis Crick in *Of Molecules and Men* [33], yet it has received much less attention in biology than Crick's other criterion, the need for organisms to reproduce and pass on 'copies' of themselves to their descendants. Here already we see a dichotomy between a complex system's natural ordering tendencies and the need (at least in living systems) to guide that order in specific ways. Coordination dynamics (Table 1) reconciles this dichotomy by viewing these two fundamental aspects as complementary ([100,104,110]).

In his general theory of nonequilibrium phase transitions called "synergetics" Haken [73] showed that close to critical points where a so-called *control parameter* crosses a threshold, very complex, high-dimensional systems can

be completely described by a much lower dimensional dynamics specified in terms of only a few collective variables or *order parameters*. What do these terms mean? *Control Parameters* refer to naturally occurring environmental conditions or intrinsic, endogenous factors that on first blush appear analogous to what an experimental scientist might call an independent variable. But the concept is entirely different, and the implications for experimental design far reaching [96]. The role of control parameters is to move the system through its repertoire of patterns and cause them to change. In fact, you only know for certain you have identified a control parameter if, when varied, it causes the system's behavior to change qualitatively or discontinuously, i. e., to change state. In a dynamical system, when a parameter changes smoothly, the attractor in general also changes smoothly. Sizeable changes in the input have little or no effect on the resulting output. However, when the control parameter passes through a critical point or threshold in an intrinsically nonlinear dynamical system an abrupt change in the attractor can occur. This sensitive dependence on parameters is called a *bifurcation* in mathematics, or a *nonequilibrium phase transition* in physical theories of pattern formation [73]. Indeed, control parameters are often referred to in mathematics as *bifurcation parameters*. Qualitative change does not mean that quantification is impossible. To the contrary, qualitative change is at the heart of pattern formation and, provided care is taken to evaluate system timescales (e. g., how quickly the control parameter is changed relative to the typical time of the system to react to perturbations; see [121]) quantitative predictions ensue that can be tested experimentally (see Sect. "The Theoretical Modeling Strategy of Coordination Dynamics: Symmetry and Bifurcations").

Collective variables are relational quantities that are created by the cooperation among the individual parts of a system. Yet they, in turn, govern the behavior of the individual parts. This is sometimes referred to as *circular* or *reciprocal causality*. In self-organizing systems the stranglehold of linear causality is broken. At best, simple cause-effect relations are the exception, not the rule. Depending on where the system lives in the space of its parameters, many causes can produce the same effect or the same cause can have multiple effects. One can intuit why the concept of collective or coordination variable is central to a science of coordination. The reason is that interactions in such systems are so complicated that understanding may only be possible in terms of system-specific collective or coordination variables. The latter are not necessarily "macroscopic quantities". In coordination dynamics, the identification of coordination variables depends on the level of

description. What is "macro" at one level may be "meso" or "micro" at another. This strategy of folding together all aspects within the dynamics of collective or coordination variables embraces the full complexity of living things on a given level of description without proliferating arbitrary divisions (for a nice discussion see [203]).

In nonequilibrium systems, the enormous compression of degrees of freedom near critical points arises because events occur on different timescales: the faster individual elements in the system become "enslaved" to the slower, "emergent" collective variables [73]. Alternatively, one may conceive of a hierarchy of timescales for various processes involved in coordination. On a given level of the hierarchy are coordination variables subject to constraints (e. g., of the task) that act as boundary conditions on the coordination dynamics. At the next level down are component processes and events that typically operate on faster timescales. Notice for the 'tripartite scheme' of Coordination Dynamics (see pp. 66–67 in [100]) the key is to choose a level of description and understand the relation between adjacent levels, not reduce to some "fundamental" lower level (Table 1). In coordination dynamics, no level is any more or less fundamental than any other. A complete description of a phenomenon always requires three adjacent tiers: The boundary conditions and control parameters that establish the context for particular coordination phenomena to occur; the collective level and its dynamics; the component level and its dynamics including the nonlinear coupling between components.

Dynamic instability is the generic mechanism underlying self-organized pattern formation and change in all (open) systems coupled to their internal or external environments [153]. Near instability the individual elements, in order to accommodate to current conditions, must order themselves in new or different ways. The patterns that emerge at nonequilibrium phase transitions may be defined as attractive states of the collective variable dynamics. That is, the collective variable may converge in time to a certain limit set or attractor solution, a nonequilibrium steady state. Attractors can be *fixed points*, in which all initial conditions converge to some stable rest state. Attractors can also be *periodic*, exhibiting preferred rhythms or orbits on which the system settles regardless of where it starts. Or, there can be so-called *strange* attractors; strange because they exhibit *deterministic chaos*, a type of irregular behavior resembling random noise, yet often containing pockets of quite ordered behavior. Stable fixed point, limit cycle and chaotic solutions as well as a wide variety of other transient and irregular behaviors are possible in the *same* system, depending on the values of control parameters (and their time dependence). Moreover, fluctua-

tions are always present, constantly testing whether a given pattern is stable. Fluctuations are not just noise; rather, by probing the stability of existing states they allow the system to discover new, more adaptive patterns that suit the prevailing circumstances (boundary conditions, control parameters; Table 1).

How might these conceptual tools aid our understanding of biological coordination? On first blush, it might seem a gigantic leap from the physics and mathematics of pattern formation in nonequilibrium systems to the problem of coordination in living things. Yet in science, analogy often plays a major role in bringing about conceptual breakthroughs. Although initially the analogy may seem far-fetched, great science often starts with a vague idea which, when followed by crucial experiments and mathematical theory renders the vague idea exact. A key aspect to appreciate is that cooperative phenomena in physical systems are typically independent of the particular molecular machinery or material substrate that instantiates them. This is because the elementary components are the same, i. e. homogeneous. On the other hand, in living, evolved things the component elements are often quite different. Thus any theory of coordination of living things will have to take into account the heterogeneity of its component elements. Perhaps as a consequence of inherent heterogeneity (and no doubt the advancement of technology) the tendency in biology is to focus more and more on specific processes at ever smaller and smaller scales. As a result, building huge data bases may sometimes appear to take precedence over finding scientific laws [55].

Finding Dynamical Laws of Coordination

What if biological coordination were shown to be a self-organized phenomenon? Might that be a springboard to finding laws of coordination? In the sense of T.S. Kuhn [131] such questions appear to call out for a new paradigm, special entry points where irrelevant details may be pruned away exposing the essential aspects one is trying to understand. Inspired by synergetics (and paradoxical though it may seem) the key to determining if coordination as a self-organized phenomenon is to focus on *qualitative change*, places where abrupt switches or bifurcations in coordination occur. Qualitative change is crucial because it affords a clear distinction between one coordination pattern and another, thereby enabling one to identify the key *collective variables or order parameters* that define coordination states and their coordination dynamics. If a complex system is changing smoothly and linearly it is hard to distinguish the variables that matter, so-called state variables, from the ones that don't. Qualita-

tive change may also be used to infer relevant quantities in more naturalistic settings. In situations where many variables may be changing in uncontrolled ways, the one(s) that change(s) abruptly are likely to be the most meaningful, both for the phenomena themselves and our understanding of them [96]. Likewise, any parameter that induces qualitative behavioral change qualifies as a *control parameter*. This is the reason why stability is so important. As a control parameter crosses a critical value the previously stable pattern becomes unstable and the system switches to a different pattern that is now stable beyond the critical point. The quite general predictions of nonequilibrium phase transition theory are a strong enhancement of fluctuations (critical fluctuations) and a strong increase in the pattern's relaxation time (critical slowing down) as the transition is approached. Obviously, if nonequilibrium phase transitions are a basic mechanism of self-organization and if, as hypothesized, the forces of evolution and self-organization form the core of biological order and coordination, it should be possible to discover nonequilibrium phase transitions and their signature features in real experiments. If not, the theory that coordination in living things is due fundamentally to self-organization must go the way of all beautiful theories that are negated by the facts.

Empirical Foundations of Coordination Dynamics: Pattern Generation, Stability and Phase Transitions

In coordination dynamics, the payoff of knowing collective variables and control parameters is high: they enable one to obtain the dynamical rules of behavior on a chosen level of description. By adopting the same strategy "one level down", the individual components and their dynamics may be studied and identified. It is the nonlinear interaction between the parts that creates coordinative patterns of the whole thereby building a bridge across levels of description (Table 1). This ability to derive phenomena from lower levels of description is at the core of what scientists usually mean by the word "understanding". In general, in complex living systems it is difficult to isolate the components and study their dynamics. The reason is that the individual components seldom exist outside the context of the functioning whole, and have to be studied as such.

If phase transitions hold the key to finding laws of coordination, where should we look for them? A central criterion for a law-based approach to coordination is reproducibility of the phenomenon in question. Although not everything is rhythmic, rhythms represent a wide variety of coordinated behaviors in a very large number of different biological systems at very many lev-

els [24,70,71,97,119,174,212,215] and seem like an obvious entry point. One only has to look at the extensive field of so-called "central pattern generators" (CPGs) in invertebrate and vertebrate neurobiology to find remarkable similarities in the patterns that living creatures produce. Terms such as "swimming" CPG, "flight" CPG, and "locomotor" CPG reflect the reproducibility of patterns and their functional significance. Synchronization and desynchronization, frequency- and phase-locking are ubiquitous features of such patterns reflecting a high degree of neural and behavioral coordination (see Sects. "History of Coordination Dynamics: Synergy and Rhythmic Order" and "Coordination of Multiple Components: From Quadrupeds to Brains").

What then of phase transitions? And what connection exists, if any, between rhythms and phase transitions? It is well-known that quadrupeds and indeed many creatures including birds and fish exhibit characteristic gaits and may switch flexibly between them depending on circumstances. In the neurobiology literature, a key question is always "where are the switches in this thing"? [1]. Rather than assume the existence of switches, a priori, the scientific approach of coordination dynamics is to investigate the necessary and sufficient conditions that give rise to switching. Inspired by theories of self-organization in nature, coordination dynamics asks if switching may take the form of a nonequilibrium phase transition. The idea is not so far fetched as it seems. Many years ago, order-order transitions were hypothesized by Erwin Schrödinger [178] to be a crucial principle of biological organization and hypothesized to be the "new laws in the organism" [109].

Three Deceptively Simple Experiments

To investigate order-order transitions experimentally, consider an experimental paradigm introduced some years ago in which human beings are asked to move their two index fingers back and forth rhythmically [94,95]. In one condition (call it parallel, Fig. 1) they are told to alternate finger movements at a comfortable rate, one finger flexing in time as the other extends. In another separate condition (call it mirror) they are told to flex both fingers together and extend both fingers together at the same time. The key part of the experiment is that participants are instructed to increase the speed at which they perform these movements. For better experimental control a pacing metronome whose frequency can be systematically increased (say every 10 cycles called a plateau) may be used for subjects to follow. The main results are shown in Fig. 1 and described in the figure's caption.
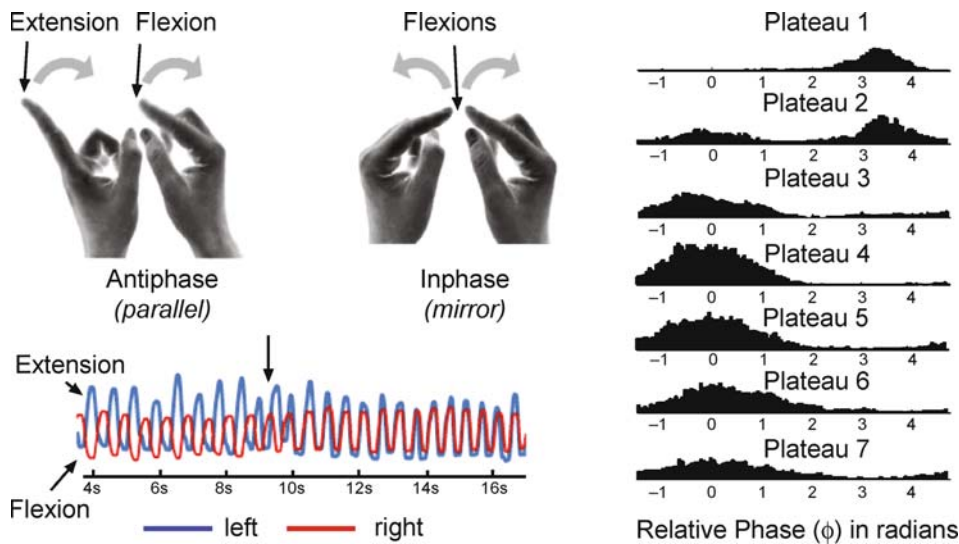
Coordination Dynamics, Figure 1

Phase transitions in bimanual movements. *Left side*. On the top are the two experimental conditions (parallel, antiphase and mirror, in phase) in the Kelso paradigm. The lower plot shows the time series of the finger movements in a representative run. As rate increases, trials initiated in the antiphase pattern spontaneously switch to the in-phase mirror pattern. The critical frequency is identified with an arrow. In contrast, trials initiated in the in-phase pattern do not switch as frequency increases (not shown). *Right side*. Distributions of relative phase between finger movements for plateaus of increasing frequency of movement. Initially the relative phase is concentrated at π radians, indicating antiphase is a stable pattern. On *plateau 2*, relative phase is concentrated around 0 and π radians, showing the bistability of antiphase and inphase coordination. For higher frequency plateaus the relative phase is concentrated at 0 radians, indicating that inphase is the only stable pattern of coordination (adapted from [7] with permission)

Experimental studies of bimanual rhythmic movement demonstrate that humans in the absence of learning procedures are able to produce two patterns of coordination at low frequency values, but only one – the symmetrical, in-phase mode – as frequency is scaled beyond a critical value. This is a remarkable result given the complexity of the nervous system, the body and their interaction with the world.

Consider another example, this time involving a human coordinating with an environmental signal [115,218]. In this experimental setup a single limb or finger is moved such that peak flexion occurs in between the beats of a pacing metronome, i. e. in a syncopated fashion. When the metronome frequency is increased, once again a critical value is reached where participants switch spontaneously to coordinating peak flexion on the beat, i. e. in a pattern of synchronization with the metronome. No such switching occurs when subjects begin in the synchronized mode of coordination. We may refer to these effects as a very basic example of *coordination between an organism and its environment*.

Now, consider the case of two people interacting with each other, an elementary form of interpersonal or *social coordination*. In this situation, each individual is instructed to oscillate a limb (the lower leg in this case) in the same or opposite direction to that of the other person [170]. In order to do the task, there must be a medium of interaction (vision, sound, touch, smell...) through which humans can couple. In this case, the two people watch each other (for details of this and other work see ▶ Social Coordination, from the Perspective of Coordination Dynamics). Then, either by an instruction from the experimenter or by following a metronome whose frequency is systematically increased, the social dyad speeds up their movements. When moving their legs up and down in the same direction, the two members of the dyad remain synchronized across a broad range of speeds. However, when moving their legs in the *opposite* direction (one person's leg extending at the knee while the other's is flexing), such is not the case. Once again at a certain critical rate participants change their behavior spontaneously so that their legs now move in the *same* direction.

The 'nonlinear' paradigm of coordination dynamics as illustrated in these three simple experiments has led to a wide range of investigations in many fields and a surprising variety of contexts (see Sect. "Collective Minds" for brief summary; also Books and Reviews) including detailed studies of underlying brain mechanisms using the full armamentarium of imaging technologies. Although
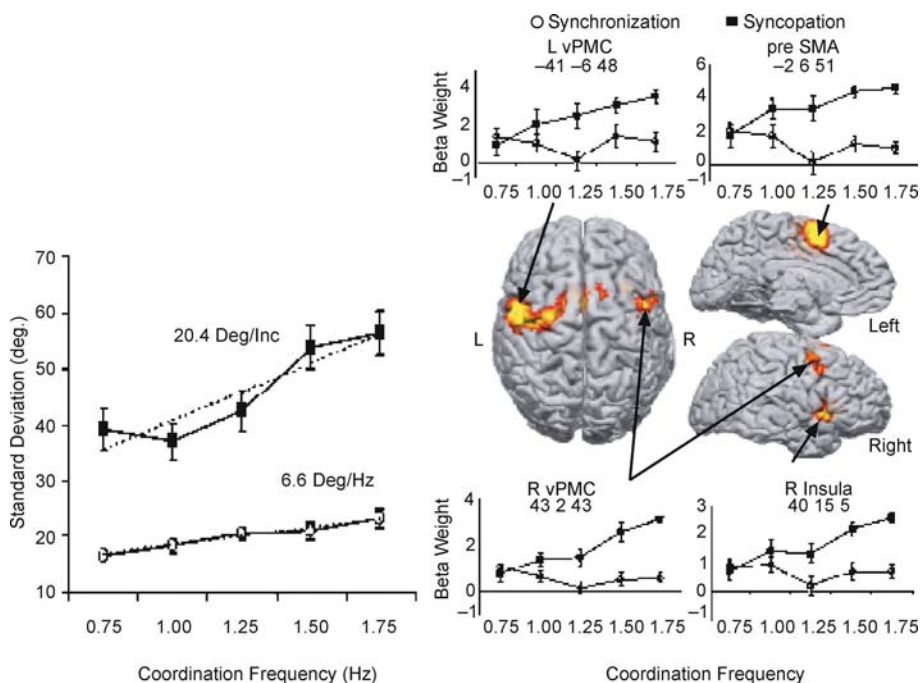
Coordination Dynamics, Figure 2
A pattern of generic results from combined brain and behavioral studies of coordination (adapted from [81]). On the *left* are behavioral results showing how relative phase variability is initially higher and increases more rapidly with the control parameter of frequency for syncopated antiphase (*filled squares*) than synchronized inphase coordination (*open circles*) with an external event. On the *right* are corresponding brain activations that comprise a network that is exquisitely sensitive to the stability of antiphase coordination. Areas depicted are left and right ventral premotor cortex (vPMC), pre supplementary motor area (pre-SMA) and right insula. The X Y Z Talairach coordinate of the peak voxel for each region is provided. Notice how the behavioral and brain data track each other

the findings would take us too far afield for present purposes ([19,20,191]; for reviews see [59,81]) two particular results are worth noting. First is that the basic paradigm has led to the first direct evidence of phase transitions in the human brain seen using both large scale electrode EEG [143,216] and SQuID arrays [35,61,62,108,123,124]. Second, and even more telling, is that fMRI evidence indicates that regardless of whether one is coordinating the two hands or coordinating with an external signal, a common network concerned with the *stability* of coordination is involved (see [81,156] for reviews).

The pattern of experimental findings described in this section illustrates an important conceptual distinction between coordination dynamics and other theories of self-organization [163]. In the latter, at bifurcation points or phase transitions, the system switches to a new, higher level of organization called a *dissipative structure*. Dissipative structures are so named because, compared with the "simpler" structures or patterns they replace, they require more energy to sustain them (ibid., p.xv). Not so in the order-order transitions of coordination dynamics. In co-

ordination dynamics, the new organization that appears at bifurcation points is 'simpler' than the one it replaces and requires less energy. For example, brain electrical activity actually drops across the antiphase to inphase transition even though the system is being driven faster [124]. In Fig. 2, blood oxygen level dependent (BOLD) activity in certain brain regions is shown to increase as the stability of the antiphase pattern decreases. It is obvious that the increasing metabolic energy demands of the brain for antiphase relative to inphase coordination will diminish once the transition to in phase occurs. Thus, the key principle behind the 'simpler' self-organizing structures that emerge in coordination dynamics are based, not (or not only) upon energy per se as in the theory of dissipative structures, but on the system's *information processing demands*. Intuitively, the antiphase pattern is more difficult to coordinate as rate or frequency is increased causing the system to switch to a pattern that is easier to perform under the current conditions. Importantly, coordination dynamics replaces vague terms such as 'task difficulty' and 'task complexity' by quantitative behavioral measures of

stability and quantitative brain measures of BOLD and neuroelectric activity.

The Theoretical Modeling Strategy of Coordination Dynamics: Symmetry and Bifurcations

The three pieces of experimental evidence described above cut across entirely different kinds of things and events (auditory, visual and proprioceptive sensations, finger and leg movements, people and brains, etc.). The common denominator is that all these things and processes are meaningfully coupled together in time under particular boundary conditions (task instructions, environmental context, manipulated parameters, etc.). The phenomena observed hint at an aspect that any basic law should exhibit, namely that although the patterns of coordination observed are realized by different physical structures and physicochemical processes, laws and regularities are abstract and relational.

How then do we go about identifying the actual underlying laws? More specifically, how do we explain the coordinative phenomena observed experimentally? As stressed above, in contrast to certain physical systems like the laser, in biological coordination the path from the microscopic level to collective order parameters is not known and cannot (yet?) be derived from first principles like conservation laws. In coordination dynamics we have to: a) identify the order parameters or coordination variables and their low-dimensional dynamics empirically; b) determine the key control parameters that move the system though its coordinative states; and c) relate different levels though a study of the individual subsystems and their nonlinear interaction.

Determining the dynamics of coordination variables is non-trivial. In all three experimental situations, the relative phase ϕ or phase relation between the component elements appears to qualify as a suitable order parameter or coordination variable. The reasons are as follows: ϕ characterizes the patterns of spatiotemporal order observed, in phase and anti-phase; ϕ changes far more slowly than the variables that describe the individual coordinating components (e. g., position, velocity, acceleration, electromyographic activity of contracting muscles, neuronal ensemble activity in particular brain regions, etc.); ϕ changes abruptly at the transition and is only weakly dependent on parameters outside the transition; and ϕ appears to obey a dynamics in which the patterns may be characterized as *attractors* or *attractive states* of some underlying dynamical system. Since in all cases the frequency or rate clearly drives the system through different coordination patterns

without actually prescribing them, frequency qualifies as a control parameter.

Determining the coordination dynamics means mapping observed, reproducibly stable patterns onto attractors of the dynamics. A general strategy is to assume sufficiently higher order dynamics and expand the vector field of these dynamics in a Fourier series:

$$\dot{\phi} = f(\phi) = a_0 + a_1 \sin(\phi) + a_2 \sin(2\phi) + \ldots \\ + b_1 \cos(\phi) + b_2 \cos(2\phi) + \ldots . \quad (1)$$

Symmetry may be used to classify patterns and restrict the functional form of the coordination dynamics. Symmetry means "no change as a result of change": pattern symmetry means a given pattern is symmetric under a group of transformations. A transformation is an operation that maps one pattern onto another, e. g. in the first experimental case, left-right transformation exchanges homologous limbs within a bimanual pattern. If all relative phases are equivalent after the transformation, then the pattern is considered invariant under this operation. Symmetry serves two purposes. First it serves as a pattern classification tool allowing for the identification of basic coordination patterns that can be captured theoretically. Given a symmetry group, one can determine all invariant patterns. Second, imposing symmetry restrictions on the dynamics itself limits possible solutions and allows one to arrive at a coordination dynamics that contains the patterns as *different* stationary states of the *same* nonlinear dynamical system. In other words basic coordination patterns correspond to attractors of the relative phase for adequate parameter values. For example, left-right symmetry of homologous limbs leads to invariance under the transformation $\phi \to \phi$ so that the simplest dynamical system that accommodates the experimental observations is:

$$\dot{\phi} = f(\phi) = -a \sin(\phi) - 2b \sin(2\phi) \quad (2)$$

where ϕ is the relative phase between the movements of the two individuals, $\dot{\phi}$ is the derivative of ϕ with respect to time, and the ratio b/a is a control parameter corresponding to the movement rate in the experiment. An equivalent formulation of Eq. (1) is

$$\dot{\phi} = -\partial V(\phi)/\partial \phi \quad \text{with } V(\phi) = -a \cos\phi - b \cos 2\phi. \quad (3)$$

In the literature, Eqs. (2) and (3) are the equations at the collective level of the HKB model of coordinated behavior, after Haken, Kelso and Bunz [76,106,139]. Figure 3 (top) allows one to develop an intuitive understanding of the behavior of Eqs. (2),(3), as well as to connect the key concepts
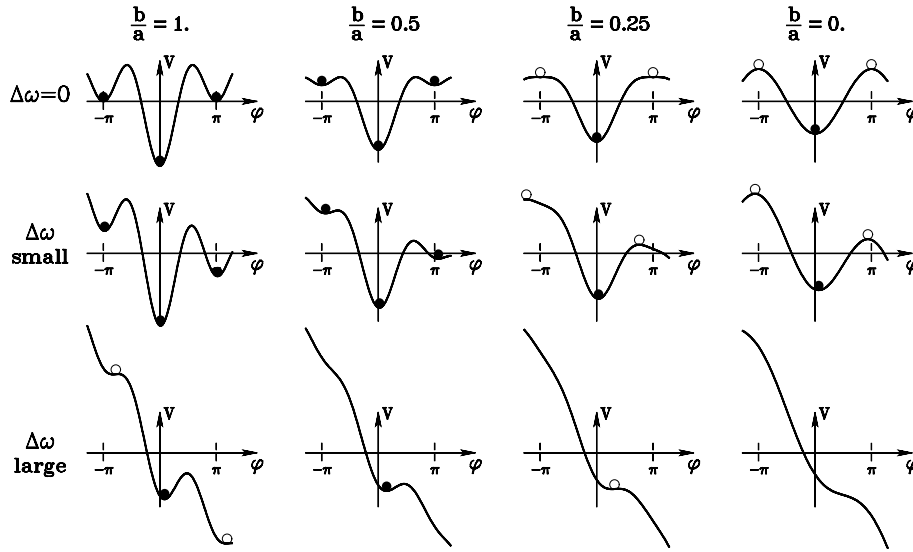
$$V(\varphi) = -\Delta\omega\,\varphi - a\,\cos\varphi - b\,\cos 2\varphi$$

Coordination Dynamics, Figure 3
The potential, $V(\phi)$ of Eq. (3) (with $\Delta\omega = 0$) and Eq. (5) (with $\Delta\omega \neq 0$). *Black balls* symbolize stable coordinated behaviors and *white balls* correspond to unstable behavioral states (see text for details)

of stability and instability in self-organized dynamical systems to the observed experimental facts.

The dynamics can be visualized as a particle moving in a potential function $V(\phi)$. The minima of the potential are points of vanishing force, giving rise to stable solutions of the elementary coordination dynamics. As long as the speed parameter (b/a) is slow, meaning the cycle period is long, Eq. (3) has two stable fixed point attractors, coordinative states at $\phi = 0$ and $\phi = \pm\pi$ rad. Thus, two coordinated behavioral patterns coexist for exactly the same parameter values, the essentially nonlinear feature of *bistability* (Table 1). Such bi- and in general multi-stability is the dynamical signature of *multifunctionality* which can be seen at many levels in living things. As the ratio b/a is decreased, meaning that the cycle period gets shorter as the system speeds up, the formerly stable fixed point at $\phi = \pm\pi$ rad becomes unstable, and turns into a *repellor* (open circles). Any small perturbation will now kick the system into the *basin of attraction* of the stable fixed point corresponding to an in-phase coordination pattern at $\phi = 0$. Notice also that once there, the system's behavior will stay in the in-phase attractor, even if the direction of the control parameter is reversed. This is called *hysteresis*, a basic form of memory in nonlinear dynamical systems.

What about the individual components? Research has established that these take the form of self-sustaining oscillators, archetypal of all time-dependent behavior [12,14,47,92,93]. The particular functional form of the

oscillator need not occupy the reader here (see ▶ Movement Coordination which uses empirical facts and symmetry arguments to restrict and thereby identify the component dynamics). More important is the nature of the nonlinear coupling that produces emergent coordination. The simplest, perhaps fundamental biophysical coupling that guarantees all the observed emergent properties of coordination: multistability, flexible switching among coordination states and primitive memory, is:

$$K_{12} = \left(\dot{X}_1 - \dot{X}_2\right)\left\{\alpha + \beta(X_1 - X_2)^2\right\}, \qquad (4)$$

where X_1 and X_2 are the individual components and α and β are coupling parameters. Notice that the 'next level up', the level of coordinated behavioral patterns and the dynamical rule that governs them (Eqs. (2) and (3)), can be *derived* from the level below, the individual components and their nonlinear interaction. One may call this *constructive reductionism*: by focusing on adjacent levels, under the boundary constraints of the task, the individual parts can be put together to create the behavior of the whole.

The basic self-organized dynamics, Eqs. (2) and (3) have been extended in numerous ways, only a few of which are mentioned here.

- *Critical slowing down* and *enhancement of fluctuations*. Introducing stochastic forces into Eqs. (2) and (3) ([175,210,211] see Chap. 11 in [74] and [101,121] for

a thorough discussion) allows key predictions of coordination dynamics to be tested and quantitatively evaluated [113,121,172]. Critical slowing is easy to understand from Fig. 3 (top). As the minima at $\phi = \pm\pi$ become shallower and shallower, the time it takes to adjust to a small perturbation takes longer and longer. Thus, the local relaxation time is predicted to increase as the instability is approached because the restoring force (given as the gradient of the potential) becomes smaller. Likewise, the variability of ϕ is predicted to increase due to the flattening of the potential near the transition point. Both predictions have been confirmed in a wide variety of experimental systems, including recordings of the human brain ([81,100,174] for review).

- *Symmetry breaking*. Notice that Eqs. (2) and (3) are *symmetric*: the dynamical system is 2π periodic and is identical under left-right reflection (ϕ is the same as $-\phi$). This assumes that the individual components are identical, which as remarked upon earlier, is seldom the case in living things where symmetries are broken all the time.

In terms of the development of the theory, an important experimental example of symmetry breaking is the case of coordinating movement with a visual stimulus: visual stimuli and limb movement are obviously not equivalent. Thus $\phi \to \phi$ symmetry cannot be assumed. This means that symmetry partners of coordination patterns with systematic phase leads or lags do not coexist at the same parameter values. To accommodate this fact, a term $\Delta\omega$ is incorporated into the dynamics [115]:

$$\dot\phi = \Delta\omega - a\sin\phi - 2b\sin 2\phi\,, \quad\text{and}$$
$$V(\phi) = -\Delta\omega\phi - a\cos\phi - b\cos 2\phi \tag{5}$$

for the equation of motion and the potential respectively.

Note that Eq. (5) falls out naturally from an analysis of the oscillators, ω_1 and ω_2, viz.

$$\dot\phi = \frac{\omega_1^2 - \omega_2^2}{2\Omega} + (\alpha + 2\beta R^2)\sin\phi - \beta R^2 \sin 2\phi \tag{6}$$

for

$$\Delta\omega = \frac{\omega_1^2 - \omega_2^2}{2\Omega} \approx \omega_1 - \omega_2 \tag{7}$$

with

$$a = -(\alpha + 2\beta R^2)$$
$$b = \tfrac{1}{2}\beta R^2\,. \tag{8}$$

Small values of $\Delta\omega$ shift the attractive fixed points (Fig. 3 middle) in an adaptive manner. For larger values of $\Delta\omega$

the attractors disappear entirely (Fig. 3 bottom) causing the relative phase to drift: no coordination between the components appears to be possible. Note, however, that the dynamics still retain some curvature (Fig. 3 bottom right): even though there are no attractors there is still attraction to where the attractors used to be. The reason is that the difference ($\Delta\omega$) between the individual components is sufficiently large that they do their own thing, while still retaining a *tendency* to cooperate. The introduction of the symmetry breaking term $\Delta\omega$ in Eq. (5) changes the entire coordination dynamics (layout of the fixed points, bifurcation structure) of the original HKB system in which $\Delta\omega = 0$. This is important to realize because it is the subtle interplay between the coupling ($k = b/a$) and the symmetry breaking term $\Delta\omega$ in Eq. (5) that gives rise to *metastability*.

Sometimes in the literature Eq. (5) is referred to collectively as the Haken–Kelso–Bunz equation. Though convenient, this is technically incorrect and fails to recognize both the intellectual contributions to its extension and the conceptual consequences thereof. For reasons of symmetry and simplicity, the original HKB equation did not contain the symmetry breaking term, $\Delta\omega$ [115] nor did it treat fluctuations explicitly [175] both of which are crucial for capturing the broad range of phenomena observed and testing further predictions. In particular, without $\Delta\omega$ there is: a) no fixed point shift, a sign of adaptation to changing circumstances, see Fig. 3 and 4; b) the bifurcation is a saddle node not, as in the original HKB equation, a pitchfork. These are different normal forms [98]; and c) most important of all, the original HKB equation does not and cannot exhibit metastability which is the key to understanding the complementary relationship between the synergic tendency of the elements to couple (integration) and at the same time to express their individual differences (segregation). The oscillators in the original HKB formulation were identical thereby excluding metastability. For these reasons, it seems wise to refer to Eq. (5) (with its stochastic aspect included) as the extended HKB equation.

Equation (5) is a bit strange. Even though it is an order parameter equation of motion that describes *coordinative* behavior (in words, phi dot is a function of phi), it includes also a parameter ($\Delta\omega$) that arises as a result of differences among the *individual components*. Equation (5) is thus a strange mixture of the whole and the parts, the global and the local, the cooperative and the competitive, the collective and the individual. Were the components identical, $\Delta\omega$ would be zero and we would not see component differences affecting the behavior of the whole (Fig. 3 top row). Equation (5) would simply reflect the behavior of the collective untarnished by component properties, a purely
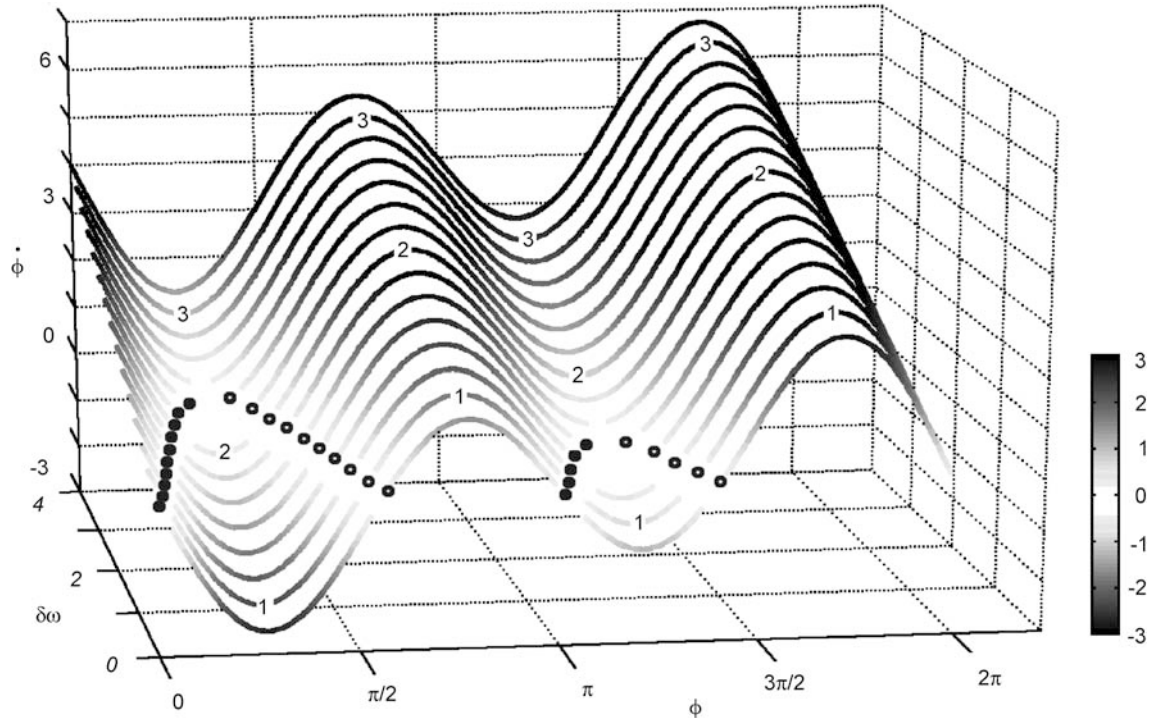
Coordination Dynamics, Figure 4
Elementary coordination law (Eq. (5)). Surface formed by a family of flows of the coordination variable ϕ (in radians) as a function of its time derivative $\dot{\phi}$ for increasing values of $\Delta\omega$. For this example, the coupling is fixed: $a = 1$ and $b = 1$. When $\dot{\phi}$ reaches zero (*flow line becoming white*), the system ceases to change and fixed point behavior is observed. Note that the fixed points here refer to *emergent coordination states* produced by nonlinearly coupled elements. 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. Three representative *lines labeled 1 to 3* illustrate the different régimes of the coordination dynamics. 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) régime of dynamics. 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 due to the loss of stability of the coordination state near antiphase, π rad. The flow now belongs to the monostable régime. Following *line 3* from left to right, no stable or unstable fixed points exist yet a subtle form of coordination – neither completely ordered (synchronized) nor completely disordered (desynchronized) – still remains. This is the metastable régime

emergent interaction – the HKB equation. It is the fact that *both* the components *and* their (nonlinear) interaction appear at the same level of description that gives rise to the array of coexisting tendencies characteristic of metastability. The history of coordination (Sect. "History of Coordination Dynamics: Synergy and Rhythmic Order") may now be seen in a new light: Eq. (5) is a basic representation of a *synergy*, a low dimensional dynamic of a metastable organization in which the tendency of the parts to act together coexists with a tendency of the parts to do their own thing (see Chap. 4 in [100]). If indeed the synergy is a unit of life and mind as proposed in [105,107] then it is metastability that endows the synergy with robustness and flexibility, enabling the same parts to participate in multiple functions.

Metastable Coordination Dynamics

From States to Tendencies

Etymologically, 'metastability', comes from the latin '*meta*' (beyond) and '*stabilis*' (able to stand). In coordination dynamics, metastability corresponds to a régime 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 coordinating components lingers at zero), but attraction remains to where those fixed points used to be (see Fig. 3, bottom row). This gives rise to a dynamical flow consisting of *both* phase trapping and phase scattering.

To best visualize the emergence of metastability, Fig. 4 shows the flow of the dynamics for the elementary coor-
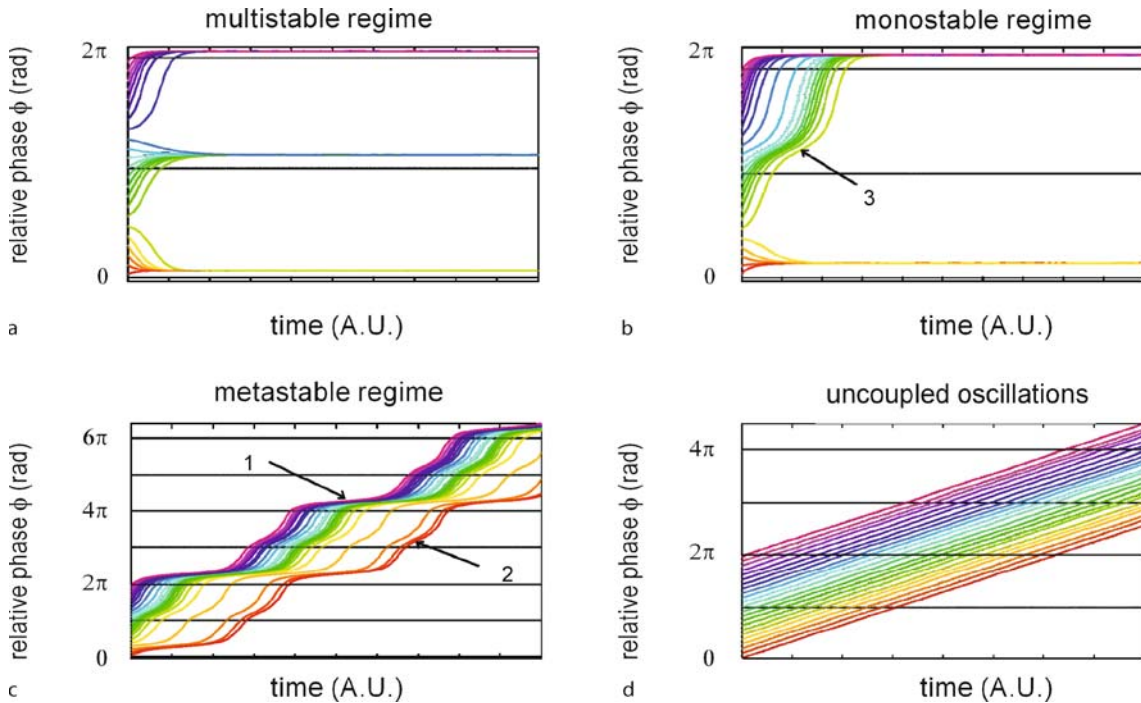
Coordination Dynamics, Figure 5
How the key coordination variable or order parameter of the elementary coordination law (Eq. (5)) behaves over time. Shown is a family of trajectories of the relative phase ϕ over time (in Arbitrary Units) arising from a range of initial conditions sampled between 0 and 2π radians, in the multistable (**a**), monostable (**b**) and metastable régimes (**c**) of Eq. (5). For the uncoupled case (**d**) the trajectories never converge indicating that the oscillations are completely independent of each other. Trajectories in the multistable régime (**a**) converge either to an attractor located slightly above $\phi = 0$ rad modulo 2π or to another attractor located slightly above $\phi = \pi$ rad modulo 2π. In the monostable régime (**b**), trajectories converge to an attractor located slightly above $\phi = 0$ rad modulo 2π. In the trajectories of relative phase for the metastable régime (**c** unwrapped to convey continuity), there is no longer any persisting convergence to the attractors, but rather a succession of periods of rapid drift (*escapes*) interspersed with periods inflecting toward, but not remaining on the horizontal (*dwells*). Note dwells near $\phi = 0$ rad modulo 2π in the metastable régime (e. g. dwell at about 4π rad annotated 1 in **c**) and nearby $\phi = \pi$ rad modulo 2π (dwell at about 3π rad annotated 2 in **c**) are reminiscent of the transient obtained for certain initial conditions in the monostable régime (Fig. 5b, annotation 3). The key point is that in the metastable régime the system's behavior is a blend of coupled and independent behavior

dination law (Eq. (5)) across a range of $\Delta\omega$ values with the coupling parameter, $k = b/a = 1$ fixed. Stable fixed points (attractors) are presented as filled circles and unstable fixed points (repellors) as open circles. Here, fixed points of the coordination dynamics correspond to phase- and frequency relationships between oscillatory processes.

The surface shown in Fig. 4 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: two stable attracting fixed points (filled circles) represent possible alternative states. Which one the system settles in depends on initial conditions and the size of the basin of attraction. In an intermediate region, following the line labeled 2 from left to right, the weakest attractor near anti-phase (right side) disappears after it collides with its associated repellor somewhere near $\Delta\omega = 1.3$, but the strongest attractor (left side) is still present as well as its repellor partner. Finally in the third region in the upper part of the surface, the dynamics become 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. Strictly speaking coordination *states* qua frequency- and phase-synchrony no longer exist in the metastable régime of the coordination dynamics. Metastability is thus a subtle blend of coupling and intrinsic tendencies in which behavior is neither completely ordered (synchronized) nor completely disordered (desynchronized). Both tendencies coexist.

How do individual and coordination behavior evolve in time in the metastable régime? A unique flow now exists in which the dynamics may be characterized by

places where the trajectory of the coordination variable converges and pauses around the horizontal and places where the trajectory drifts or diverges from the horizontal. Let us define the former as a *dwell time*, and the latter as an *escape time*. In Fig. 5c we show two locations for the dwell times: one that lingers a long time before escaping (e. g. Fig. 5c, annotation 1) slightly above the more stable in-phase pattern near 0 rad (modulo 2π), and the other that lingers only briefly (e. g. Fig. 5c, annotation 2) slightly above π (modulo 2π). These inflections recur over and over again as long as the system self-organizes in the metastable régime, i. e. as long as it does not undergo a phase transition to a locked or unlocked state. Despite the complete absence of phase-locked attractors, the coordinating elements in the metastable régime do not behave totally independently. Rather, their interdependence takes the form of dwellings (phase gathering tendencies) nearby the remnants of the fixed points (cf. Fig. 3 bottom; Figs. 4, 5c) and may be nicely expressed by concentrations in the histogram of the relative phase (see Chap. 4 in [100]).

Recently metastability has been hailed as a "new principle" of coordination in the brain and has been embraced by a number of neuroscientists as playing a role in various cognitive functions, even consciousness itself (e. g. [44,45,57,58,111,127,187,212]). According to a recent review [49]:

> *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 as they exhibit tendencies for coordinated activity* [19,20,97,100].

For Coordination Dynamics, metastability's significance lies not in the word itself but in what it means for understanding coordination in living things. In coordination dynamics, as shown in its most elementary form (Eq. (5)), metastability is not a concept or an idea, but a direct result of the broken symmetry of a system of (nonlinearly) coupled (nonlinear) oscillators. Such a design principle for the brain seems highly plausible given that rhythms in the brain are ubiquitous, operate over a broad range of frequencies and are strongly associated with various sensory, motor and cognitive processes [10,24,100].

The Creation of Information

There is another reason for proposing metastable coordination dynamics as the essential way the brain and perhaps all complex organizations work. It concerns an analogy to how physicists understand how we know the universe we live in. According to Quantum Mechanics, out of a universe in which quantum indeterminacy rules – the wave function is spread out over all of space – nature selects an alternative. Information is thereby created. The way this is done in practice is that a device is built in which an interactive material is placed in a physically, electrically or chemically metastable state. According to the late quantum measurement theorist, H.S. Greene [69]:

> *It is the observable transition between this metastable state and a more stable state that conveys the essential information concerning a sub-microscopic event that would otherwise go undetected … The functional material of the detector must be macroscopic and in a metastable state which allows the quantal interaction to become manifest at the macroscopic level.*   (see p. 173 in [69])

This is how some physicists view the creation of information: bit from it, as it were (in contrast to John Archibald Wheeler's 'it from bit'). Quantum Mechanics thus implies the creation of new information in the process of measurement and observation. Likewise, we have seen in the human brain that information (as a marginally coupled, phase-locked state) is created and destroyed in the metastable régime of the coordination dynamics, where tendencies for apartness and togetherness, individual and collective, segregation and integration, phase synchrony and phase scattering *coexist*. New information is created because the system operates in a special régime where the slightest nudge will put it into a new coordinated state. In this way, the (essentially nonlinear) coordination dynamics creates new, informationally meaningful coordination states that can be stabilized over time. The *stability of information over time* is guaranteed by the coupling between component parts and processes and may constitute a dynamic kind of (non-hereditary) memory. It does not seem a big step then to say that once created, this information can then guide, modify and direct the system's dynamics. As we shall see in Sect. "Modifying Coordination: Meaningful Information" studies of intentional change, environmental change, learning and so forth have demonstrated both empirically and theoretically that an intentional goal – as memorized information – acts in the same information space as the coordination dynamics ([114,173]; see also [141]).

### Coordination of Multiple Components: From Quadrupeds to Brains

Phase- and frequency synchronization, the coupling among oscillatory processes, are an example, par excel-

lence, of self-organization in natural systems [76,119,132, 161,219]. Think of the famous clocks on the wall, no two exactly the same in frequency, but somehow ticking perfectly in time with each other. The weakest of coupling, whether through vibration in the wall or displacement of the air, enables the clocks to be mutually coordinated without any coordinator at all. Similar phenomena have been seen in the brain and have been hypothesized to play a key role in "binding": oscillations in the brain appear to be coupled or "bound" together into a coherent network when people attend to a stimulus, perceive, think and act (e. g., [34,43,67,184,214]). For example, synchronization in the so-called gamma band (approx. 30–50 Hz) has been proposed as a neural correlate of consciousness. The Journal *Science* announced the synchronization effects observed in monkey cortex as "The Mind Revealed" (see also [34]).

The brain, it seems, has latched on to phase synchrony as a principle of self-organization. Though the connection is seldom made, phase- and frequency- synchronization is typical of central pattern generators (CPGs), neural circuits in vertebrates and invertebrates that generate timing sequences without feedback from the periphery or the help of reflexes (see Sect. "Empirical Foundations of Coordination Dynamics: Pattern Generation, Stability and Phase Transitions"; [70,71]). Indeed, it is the temporal order observed that allows us to talk about 'pattern generators' in the first place. Though the specific mechanisms are obviously different between the visual cortex of the monkey and the stomatogastric ganglion of the lobster, the dynamic patterns are the same, hinting at the source of an underlying principle [97,100,174]. But what form might the coordination dynamics of the brain take?

Obviously when it comes to the brain there are, in principle, very many regions to coordinate. In practice, however, only a restricted set of regions appear to be functionally connected during particular tasks (see, e. g. Fig. 2). The idea, then, is that one could use the Central Pattern Generator (CPG) design for quadrupedal locomotion [32,66,176] as a basic model of interaction among cortical pattern generators. This is not as far fetched as it seems. It is likelier than not that the precursors to the structure and function of the cerebral cortex are self-contained circuits in the spinal cord and brainstem that generate intrinsic patterns of rhythmic activity [70,71,220]. Such CPGs typically work by transforming tonic driving inputs into detailed spatiotemporal patterns of (usually oscillatory) activity. Several of the properties of CPGs are conserved throughout evolution rendering them a likely candidate for the basic building blocks of the brain [72]. The hypothesis proposed here is that cortical pattern genera-
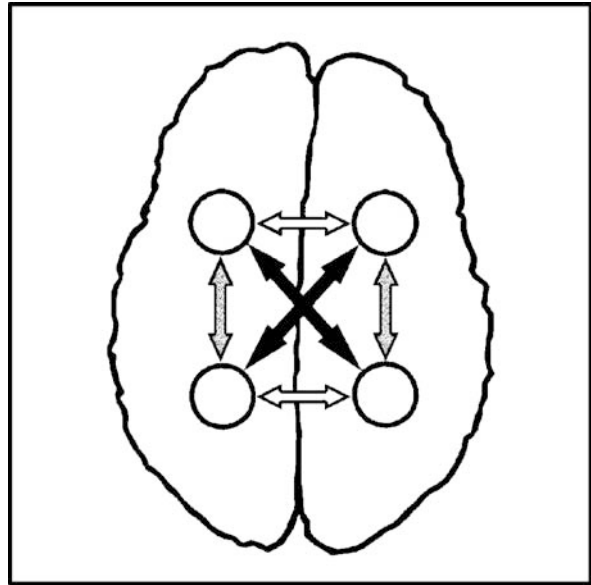
Coordination Dynamics, Figure 6
A schematic of brain coordination dynamics among four brain regions. Each *circle* represents an area of the brain capable of intrinsic oscillation and the *arrows* correspond to connections among brain areas giving rise to cortical pattern generation (see text)

tors may underlie the coordination that is needed for everything the brain is purported to do – think, feel, remember, act, socialize, etc.

Following the footsteps of basic coordination dynamics, in the quadruped analogy each "limb" corresponds to a neural region capable of intrinsic oscillatory activity and the patterns emerge from (broken) symmetries and changes in coupling between neural regions. For example, Fig. 6 shows a cartoon of the neuroanatomical connections underlying the anterior-posterior coordination of the hemispheres of the brain.

The relevant variables are four phase variables, ϕ_{ij} (with $i \in$ {right, left hemisphere}, $j \in$ {anterior, posterior} characterizing the oscillatory behavior of each brain area with respect to its timing. Much research on coordination dynamics shows that the *relative phase* is a key coordination variable or order parameter although it is quite possible that amplitudes and frequencies are important variables too [4,57,111]. For the sake of simplicity, we stick to the case of interareal cortical coordination between 4 brain regions, where a set of 3 relative phases suffices to characterize any pattern uniquely.

As already illustrated, a key notion is to use symmetry to classify patterns and restrict the functional form of the coordination dynamics. Here, pattern symmetry means

a given cortical pattern is symmetric under a group of transformations. As we have noted, a transformation is an operation that maps one pattern onto another, e. g. the anterior-posterior (a-p) transformation exchanges anterior and posterior regions within a cortical pattern. If all relative phases are equivalent after the transformation, then the pattern is considered invariant under this operation.

Symmetry serves as a pattern classification tool allowing for the identification of basic cortical patterns that can be captured theoretically. Given a symmetry group, one can determine all invariant patterns. For example, certain idealized cortical patterns are invariant under the symmetry group generated by the following operations: exchange of anterior and posterior, exchange of left and right, and inversion of all phases (inversion of time). A good way to illustrate these patterns is with phase pictograms.

Imposing symmetry restrictions on the dynamics itself limits possible solutions and allows one to arrive at a coordination dynamics that contains the patterns as *different* stationary states of the *same* nonlinear dynamical system. In other words basic cortical patterns correspond to attractive states of the relative phase for adequate parameter values:

$$\dot{\phi}_{ij} = \sum_{n=1}^{\infty} \{A_n \sin(n(\phi_{ij} - \phi_{\hat{i}j}))$$

$$\text{Homologous contralateral coupling (white arrows)}$$

$$+ C_n \sin(n(\phi_{ij} - \phi_{i\hat{j}})) \tag{9}$$

$$\text{Ipsilateral coupling (gray arrows)}$$

$$+ E_n \sin(n(\phi_{ij} - \phi_{\hat{i}\hat{j}}))\}$$

$$\text{Nonhomologous contralateral coupling (black arrows)}$$

where A_n, C_n and E_n are parameters and a hat over an index means that the opposite value is taken, e. g. if $i = $ right, then $\hat{i} = $ left.

To analyze the solutions to the phase dynamics, for the sake of simplicity the coordination dynamics may be restricted to second order. Higher orders generate parameter régimes where many patterns may coexist; first order removes the possibility that some patterns may coexist. Also, diagonal coupling (black arrows in Fig. 6) may be neglected by setting $E_n = 0$. Notice that an effective diagonal coupling still exists because two couplings are sufficient to stabilize any pattern of activity among 4 cortical areas. Moreover, it is easier to generalize a system with contralateral and ipsilateral couplings to systems in which more areas are involved.

In sum, following exactly the basic theoretical modeling strategy (Eq. (1)) the dynamical system takes the following form:

$$\dot{\phi}_{rp} = A_1[\sin(\phi_{rp} - \phi_{lp}) + \sin(\phi_{la})]$$
$$+ A_2[\sin(2(\phi_{rp} - \phi_{lp})) + \sin(2\phi_{la})]$$
$$+ 2C_1 \sin(\phi_{rp}) + 2C_2 \sin(2\phi_{lp})$$
$$\dot{\phi}_{lp} = A_1[\sin(\phi_{lp} - \phi_{rp}) + \sin(\phi_{la})]$$
$$+ A_2[\sin(2(\phi_{lp} - \phi_{rp})) + \sin(2\phi_{la})]$$
$$+ C_1[\sin(\phi_{lp} - \phi_{la}) + \sin(\phi_{rp})] \tag{10}$$
$$+ C_2[\sin(2\phi_{lp} - \phi_{la})) + \sin(2\phi_{rp})]$$
$$\dot{\phi}_{la} = 2A_1 \sin(\phi_{la}) - \phi_{lp}) + 2A_2 \sin(2\phi_{la})$$
$$+ C_1[\sin(\phi_{la} - \phi_{lp}) + \sin(\phi_{rp})]$$
$$+ C_2[\sin(2(\phi_{la} - \phi_{lp})) + \sin(2\phi_{rp})] .$$

Solving $\dot{\phi}_{ij} = 0$ yields stationary solutions that correspond to idealized cortical "gaits". Trot, pace, gallop and jump patterns may be identified as multistable or monostable solutions in various parameter régimes. Patterns of lower symmetry can also be captured. Obviously the foregoing analysis is intended for illustrative purposes only. The examples provided in Fig. 7 and 8 are only a few of very many possible cortical patterns that can be obtained by further symmetry groups. It is important to empha-
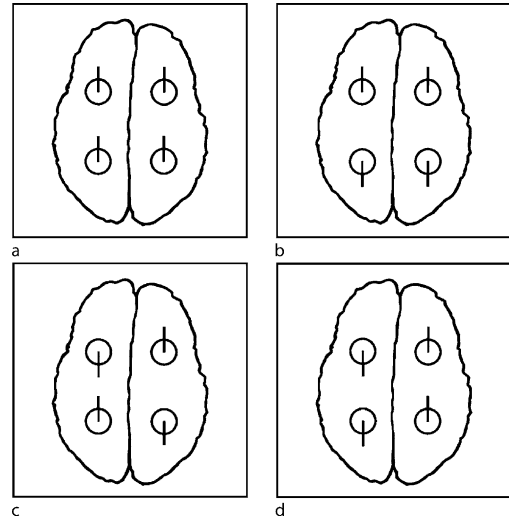
Coordination Dynamics, Figure 7
Brain phase pictograms. Each brain area is represented as a *circle*. The spatial arrangement of the circles viewed from looking down on the top of the head represents the brain's hypothesized anterior-posterior and left-right functional organization. Phase is represented by the angle the stick makes on each circle, with the reference phase being zero for the right frontal region. If all phases are rotated by the same amount in the same direction, the cortical coordination pattern remains the same. The patterns in a, b, c and d are those idealized cortical patterns that remain invariant under anterior-posterior, left-right and time inversion operations. Notice that the relative phase between any two brain regions is either inphase or antiphase

size that not all patterns in a given symmetry group are observable. Which ones are actually observed is dictated by the coordination dynamics, in particular a given pattern's *stability* which, as we have seen, can be measured (cf. Sect. "Empirical Foundations of Coordination Dynamics: Pattern Generation, Stability and Phase Transitions"). As in the simpler cases of coordination dynamics described above, *switching* among cortical patterns is due, not to switches per se but to instabilities – phase transitions or bifurcations in the phase dynamics. Neuromodulators are candidate control parameters capable of sculpting cortical patterns by leading the system through instabilities [130]. Moreover, when the oscillatory frequencies in the anterior and posterior regions of the brain are slightly different, a kind of partial coordination among cortical regions may occur. This is exactly the *metastable* coordination dynamics of the brain as described in the previous section. Here again, the key point is that the rules of the game appear to be run by principles of coordination dynamics and symmetry. As always, experiments are now needed to test this hypothesis. EEG measures of cross-frequency phase synchrony of the human brain may reflect a start in this direction (e. g., [84,158]). More direct attempts are underway in our laboratory [199].

Coordination Dynamics, Figure 8
Representative brain phase pictograms corresponding to cortical patterns of lower symmetry. Here the anterior-posterior symmetry is dropped and the cortical patterns that remain form two one parameter families. One family consists of in-phase ordering *within* anterior and posterior areas and any fixed phase relation *between* anterior and posterior regions (**a,b**). The other family (**c,d**) consists of anti-phase relations within frontal and anterior regions and any fixed phase relations between them
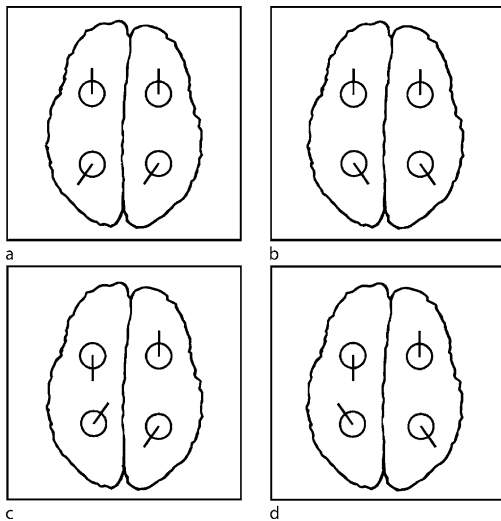
"Collective Minds"

The basic coordination dynamics for two and four nonlinearly interacting components (Eqs. (2)–(10)) can readily be elaborated as a model of emergent coordinated behavior or "group cohesion" among very many anatomically different components (see, e. g. [5]). Self-organized behavioral patterns such as singing in a group or making a "wave" during a football game are common, yet unstudied examples. By virtue of information exchange nearest neighbors adjust their motions to each other generating, and being influenced by, their social environment. Recently, Néda and colleagues [148,149] have examined a simpler group activity: applause in theater and opera audiences in Romania and Hungary. After an exceptional performance, initially thunderous incoherent clapping gives way to slower, synchronized clapping. Measurements indicate that the clapping period suddenly doubles at the onset of the synchronized phase, and slowly decreases as synchronization is lost. This pattern is a cultural phenomenon in many parts of Europe: a collective request for an encore. Increasing frequency (decreasing period) is a measure of the urgency of the message, and culminates in the transition back to noise when the performers reappear. These results are readily explained by a model of a group of globally coupled nonlinear oscillators [132]:

$$\frac{\mathrm{d}\phi_k}{\mathrm{d}t} = \omega_k + \frac{K}{N} \sum_{j=1}^{N} \sin(\phi_j - \phi_k) \qquad (11)$$

in which a critical coupling parameter, K_c determines the different modes of clapping behavior. K is a function of the dispersion (D) of clapping frequencies:

$$K_c = \sqrt{\frac{2}{\pi^3}} D . \qquad (12)$$

During fast clapping, synchronization is not possible due to the large dispersion of clapping frequencies. Slower, synchronized clapping at double the period arises when small dispersion appears. Period doubling rhythmic applause tends not to occur in big open-air concerts where the informational coupling among the audience is small. K can also be societally imposed. In Eastern European communities during communist times, synchronization was seldom destroyed because enthusiasm was often low for the "great leader's" speech. For people in the West, the cultural information content of different clapping patterns may be quite different. Regardless, the mathematical descriptions for coordinated behavior – of social dyads and the psychology of large groups – are remarkably similar.

Modifying Coordination: Meaningful Information

Unlike the behavior of inanimate things, the self-organizing dynamics of animate behavior is based on information (Table 1), though not in the standard sense of data communicated across a channel [180]. In coordination dynamics, *collective or coordination variables are context-dependent and intrinsically meaningful*. Context-dependence does not imply subjectivity and lack of reproducibility. Nor does it mean that every new context requires a new collective variable or order parameter. As we have seen already, for example, within- and between-person coordinated behaviors are described by the same self-organizing coordination dynamics. One of the consequences of identifying the latter is that in order to *modify or change* the system's behavior, new information (in the form say, of an environmental input, a task to be learned, or an intention to change behavior) is expressed in terms of parameters acting on system-relevant collective dynamics. On the one hand, the benefit of identifying collective variables is that they embrace the full complexity of the system and hence provide the relevant information about *what* to modify. On the other, the collective variable dynamics – prior to the introduction of any new information – influences how that information can be used. The upshot is that information is not lying out there as mere data: information is meaningful to the extent that it modifies, and is modified by, the collective variable dynamics.

A minimum mathematical form for the full coordination dynamics which encompasses both spontaneous self-organizing tendencies and specific parametric influences is

$$\dot{\phi} = f(\phi) + f\inf(\phi) \qquad (13)$$

where the first term is the typical so-called "intrinsic dynamics" e. g., of Eq. (5) or Eq. (10) and the second term represents 'informational forcing', i. e., a perturbation of the vector field of the dynamics attracting the system toward a required coordination pattern. It is important to emphasize that the plus sign in Eq. (13) is for operational purposes only, affording the measurement of the complementary contributions to the coordination dynamics of both spontaneous and directed (parametric) influences. The conceptual advantage of Eq. (13) is that information acts in the same space as the collective variables that define the intrinsic coordination patterns, i. e., those patterns that characterize spontaneous coordination tendencies. Thus, information is not arbitrary with respect to the dynamics. A corollary of this formulation is that information has no meaning outside its influence on the intrinsic dynamics. They are cut, as Sheets-Johnstone [182] remarks, from the same dynamic cloth.

Intentional Dynamics

Self-organizing processes, in the manner of Haken's synergetics, provide a theoretical foundation for all forms of coordination. However, we do not want to throw the baby out with the bathwater. Coordinated behavior often has a goal-directedness to it as well. We humans, for example, have no doubt whatsoever that it is us, and us alone, that direct the motions of our own bodies. Where do agency and directedness come from? A clue comes from considering the elementary spontaneous movements we are born with which consist of a large repertoire of spontaneous (thus self-organized) movements – making a fist, kicking, sucking, etc. etc. Only at some point does the child realize – through his own movements and the kinaesthetic sensations they give rise to – that these movements are his own. If one attaches the string of a mobile to his foot, he comes to realize that it is *his* kicking movements that are causing the mobile to move in ways that *he* likes. The pre-existing repertoire enables activities to happen before we make them happen. Evolutionarily constrained self-organizing coordination tendencies ('intrinsic dynamics') thus appear to lie at the origins of conscious agency. They are, in the words of the philosopher Maxine Sheets-Johnstone, "the mother of all cognition", presaging every conscious mind that ever said "I". From spontaneous self-organized behavior emerges the self – "I am" "I do" and from there a huge range of potentialities ('I can do'). "I-ness" arises from spontaneity, and it is this "I" that directs human action. As Sheets-Johnstone [182] cogently remarks, we literally discover ourselves in movement. In our spontaneity of movement, we discover arms that extend, mouths that open, knees that flex and so forth. We make sense of ourselves as living things.

Following these insights, consider briefly how Coordination Dynamics addresses the role of intentional information in bringing about behavioral change. How is the process of intentionally switching among patterns of coordination to be understood? According to the theory, the relative stability of the intrinsic patterns plays a role in determining how easily the system can switch in and out of coordination states. As defined previously, "intrinsic dynamics" expresses the fact that the system (which may include the brain) – prior to any specific input – already possesses a repertoire of behavioral patterns that are unique to each individual. Theoretically, intention parametrizes the intrinsic dynamics in two ways: (i) by destabilizing an ongoing pattern and stabilizing a target pattern [114,137,171]; and (ii) by stabilizing an intrinsically unstable pattern that under the current circumstances might otherwise become unstable and switch (see

Chap. 5 in [100], [114]). Measurement of switching time shows that intention both acts upon and is constrained by the intrinsic dynamics of coordination. First, the system switches far faster from less stable to more stable patterns (as measured by variability) than vice-versa. Second, the data show that it is possible to intentionally stabilize intrinsically unstable patterns under conditions in which they would normally switch. Both results are in excellent agreement with theory [114,171,173].

The neural basis of the interaction between intrinsic brain dynamic activity and *intentional* pattern selection and switching is just beginning to be studied and the results look very promising [39]. *Spontaneous* switching between patterns is known to be associated with increased activity in prefrontal, premotor and parietal regions [3,37,146], a network that is compatible with the stability dependent circuits described in Fig. 2 (see also Jantzen & Kelso, 2007). Increased activity reported in specific brain regions appears to reflect the loss of pattern stability that precedes spontaneous pattern switching. New results from our laboratory show that there is greater activity in the basal ganglia (BG) – a region known to be crucial for starting and controlling voluntary movements [68] – when moving from a more to a less stable pattern [39]. The heightened level of activity in BG may be related to the stability of the original pattern, the stabilization of the selected pattern switched into or both. Regardless, this intriguing result suggests that the basal ganglia play a key role in parametrizing the coordination dynamics.

Stimulus (Parametric) Stabilization and Change

Not only internally generated information is able to stabilize and destabilize coordination states under suitable circumstances: coupling sound, vision or touch conditions to specific aspects of an individual movement have been shown, not only to modify the movement but to *globally* stabilize coordination [25,50,122,133]. Thus the role of 'stimuli' in Coordination Dynamics is much more than to trigger preset motor commands or provide feedback to the motor system. To account for these kinds of effects, Jirsa and colleagues [89] introduced the notion of *parametric stabilization*: coupling specific sensory input parametrically to a set of limit cycle oscillators (see also [4,91]):

$$\ddot{x}_1 + f(x_1, \dot{x}_1)\dot{x}_1 + \omega^2 x_1 = g(x_1, \dot{x}_1, x_2, \dot{x}_2) + \varepsilon(t)x_1$$
$$\ddot{x}_2 + f(x_2, \dot{x}_2)\dot{x}_2 + \omega^2 x_2 = g(x_2, \dot{x}_2, x_1, \dot{x}_1) + \varepsilon(t)x_2$$

$$(14)$$

where f is a nonlinear oscillator function, g represents the HKB coupling (Eq. (4)), ω is the eigenfrequency of the oscillator and $\varepsilon(t)$ represents sensory information. Here again in Eq. (14) we see a key aspect of coordination dynamics, namely that perception and action, sensory information and the dynamics of movement are inextricably linked. Notice the linkage in this case is of a parametric, multiplicative nature which is necessary to account for both the local changes to component trajectories produced by sensory information (called 'anchoring') and the global stabilization effects on the coordination dynamics. Fink et al. [50] for example, were able to show that such localized and specific sensory information was capable of shifting (and thereby delaying) the critical point at which phase transitions occurred.

A Brief Survey of Applications and Elaborations of Coordination Dynamics

The foregoing discussion pertains to just two of the many kinds of adaptive modification of coordination dynamics that have been investigated in the literature. Here only a flavor can be provided. The sample includes, but is by no means limited to: the processes underlying the ability of biological systems to stabilize intrinsically unstable systems [26,54,199]; the initiation (including 'false starts') and coordination of discrete, discontinuous behaviors [52,80,86,112,188,189] including neurally-based comparisons with those of a continuous, rhythmic nature [166,185]; the spontaneous recruitment and annihilation of biomechanical degrees of freedom to accomplish task and environmental conditions [21,23,51,118]; the coordination dynamics of trajectory formation [22,38] and cursive handwriting [6]; the important role that perception [145] and attention [2,27,147,190,193,194] play in modulating coordinative stability; how practice and learning alter the entire coordination repertoire by reshaping the landscape of the coordination dynamics using competitive and cooperative mechanisms [53,140,151, 177,222,223]; the stabilization and consolidation of new memorized states of coordination and the dynamics of the forgetting process [128,129]; how handedness amplifies asymmetries in the coordination dynamics [2,201], and so forth. The same concepts and methods have been applied to problems ranging from maintaining posture and stabilizing postural sway [8,9,42,83] to understanding how concurrent cognitive tasks modulate coordination dynamics [159,183].

Theoretical research at the neural level has progressed from phenomenological modeling at behavioral (e. g. [60,76,89,115,118,175,201]) and brain levels [88,205] to neurobiologically-grounded accounts of both unimanual [56,63,125] and bimanual coordination [87] that are

based on known cellular and neural ensemble properties of the cerebral cortex. Recent work [85] has extended this neural theory to include the heterogeneous connectivity between neural ensembles in the cortex. Once general laws of coordination at behavioral and brain levels have been identified, it has proved possible to derive them from a deeper theory founded on neuroanatomical and neurophysiological facts, thereby causally connecting different levels of description [117] for review). The neural theory, in turn, poses a number of challenges to experiment, such as how synaptic and cellular properties are influenced by learning, arousal and attention [103].

Remarkable applications of coordination dynamics have occurred in expected directions (though none the less remarkable for all that) including many physical activities and sports such as the relation between respiration and locomotion [36], juggling [13,79], gymnastics [142], running [41], tennis [157], swimming [179], boxing [135], skiing [154], golf [125] and even riding horses [134] to name only a few, as well as in entirely unexpected directions, such as modeling coordination of infant breathing as a way to understand the effects of premature birth [65], studies of coordination dynamics in children with Developmental Coordination Disorder [213] and the introduction of coordination dynamics therapy to treat a wide variety of CNS disorders and diseases (e. g. [167,168,169]; see also [207]). Principles of coordination dynamics have been shown to apply to perceptual grouping as nicely illustrated by the classic bistable properties of reversible figures such as the Necker cube (e. g. [100]), pattern recognition [77], the visual perception of spatiotemporal inphase and antiphase moving stimuli [18,40,78,221] and speech categorization [28,202]. In many cases the foregoing research findings have expanded, if not overturned, conventional explanations of phenomena that have seldom considered dynamics.

Increase in research activity using the concepts and methods of coordination dynamics has been such that the term has taken on a life of its own in different fields. Thus, it is commonplace in the literature to hear the words 'cognitive', 'brain', 'neural', 'social', 'behavioral', 'developmental' 'multimodal', 'postural', etc., qualify and precede the words *coordination dynamics*. The dynamical approach is currently center stage in a number of fields, for example, dynamical neuroscience (e. g., [90,160]), dynamical cognitive science (e. g., [16,162,186,209]), behavioral [217] and task [165] dynamics, dynamical social psychology (e. g., [15,155,206]), dynamical systems accounts of development (e. g., [135,149,191,192,204]; see also [195]) and its implications are under careful consideration in philosophical circles (e. g. [11,29,30,31,198]).

Future Directions and Conclusions: The Complementary Nature of Coordination Dynamics

General laws and principles of biological coordination – to the extent they exist – are, by definition, abstract and mathematical. Yet, these laws are always conditioned by and realized by specific mechanisms and contexts. Over the last twenty-five years, often using the field of animate movement as an entry point it has been shown that the same coordination dynamics applies to functional coordination in a wide variety of situations. Although the basic laws for a quantitative description of the phenomena observed when human beings (and human brains) move, interact with the environment and with each other are the same, the anatomical, mechanical and physiological mechanisms realizing these dynamics are obviously not. Laws and mechanisms are complementary aspects of coordination dynamics.

Current research and theory views coordination as arising from the mutual interplay of constraints on multiple levels of description – ranging from the intrinsic properties and modes of interaction among cells and cellular ensembles in brain circuitry to biomechanical influences at the behavioral level all the way to cognitive and task constraints. Coordination dynamics is not only a theoretical framework, but also a research program that explicitly attempts to incorporate and connect known constraints at multiple levels of description. For instance, coordination dynamics successfully identified and later quantified the form of the nonlinear coupling among interacting components. In showing that the stability and change of coordination is due to nonlinear interactions among individual components coordination dynamics removes some of the mysticism behind the contemporary terms "emergence" and "self-organization". At the same time, coordination dynamics expands and modifies the concept of self-organization in non-living systems by introducing new concepts to account for the fact that coordination is not only characterized by self-organization but also by directed or supervised forms of coordination. The two origins or cornerstones of coordination dynamics may be reconciled by showing how meaningful information originates from self-organizing processes and may in turn modify them.

In studies of coordinated movement, the field to which coordination dynamics owes its origins, it has proven useful to try to isolate the role of various constraints and how they are mediated by the central nervous system. On the one hand, this strategy has helped identify different factors that serve to stabilize coordination under conditions in which it may otherwise become unstable and susceptible to change. On the other hand, a focus on iso-

lating particular constraints can lead, albeit unwittingly, to dichotomies (e. g., coordination principles versus neuromuscular-skeletal mechanisms of implementation) that may not be so useful. In reality it seems safe to conclude that a coalition of constraints – acting on multiple levels – impinges upon the stability of coordination depending on task and environmental context and the mover's intent. For example, the multilevel theory offered by Kelso [100] connects task goals (Level 1) to constraints on nonlinear oscillators (Level 3), the interactions among which determine the coordinative patterns observed (Level 2). Thus, rather than pose "abstract laws of coordination dynamics" against "neuromuscular-skeletal determinants of coordination", more important is to understand how the balance between identified constraints plays itself out in the course of any coordinated activity. Situations in which constraints are placed in competition with each other often prove to be highly revealing [122].

Throughout this article, every effort has been made to articulate the key notions of coordination dynamics, both conceptual and technical, and to present them in close proximity in order to help both the novice and the expert reader. The behavioral simplicity of the basic coordination patterns studied in the laboratory is deceptive; their understanding, however, requires recent advances in physics and mathematics. The theoretical concepts and methods of coordination dynamics are likely to play an ever greater role in the social, behavioral, economic, cognitive and neurosciences, especially as the interactions among disciplines continues to grow. Up to now, the use of nonlinear dynamics is still quite restricted, and often metaphorical. One reason is that the tools are difficult to learn, and require a degree of mathematical sophistication. Their implementation in real systems is nontrivial, requiring a different approach to experimentation and observation. Another reason is that the dynamical perspective is often cast in opposition to more conventional theoretical approaches, instead of as an aid or complement to understanding. The former tends to emphasize decentralization, collective decision-making and cooperative behavior among many interacting elements. The latter tends to focus on individual psychological processes such as intention, perception, attention, memory and so forth. Yet there is increasing evidence that intending, perceiving, attending, deciding, emoting and remembering have a dynamics as well. The language of dynamics serves to bridge individual and group processes. In each case, dynamics must be filled with content, with key variables and parameters obtained for the systems under study. A beauty about coordination dynamics is that the coordination variables or order parameters are semantic, relational quantities that

"enfold" different aspects together thereby reducing often arbitrary divisions. Every system is different, but what we learn about one may aid in understanding another. What may be most important of all is to see animated living things in the light of a theory – coordination dynamics – that embraces both spontaneous self-organizing and directed processes, the complementary nature.

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