J.A. Scott Kelso's Contributions to Our Understanding of Coordination

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1 Introduction

"Does old Scotty still make a living from finger wagging?" A question asked by an Irish man who had known Scott Kelso since both were children. The answer: "Yes, and doing quite well, actually" triggered the much tougher question: "What can be studied there for half a life span?" Such was not possible to respond in detail as we were at the airport in Miami and had to catch our flights. But the question remains, in more scientific terms: why do we study coordination dynamics? Why are not only psychologists and kinesiologists but also theoretical physicists interested in finger wagging? Theorists appreciate laws and first principles, the more fundamental, the better. Coordination dynamics provides such laws. They are 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.

2 Elementary Coordination Dynamics

The most basic phenomenon in coordination dynamics is easy to demonstrate: When humans move their index fingers in an anti-phase coordination pattern (one finger flexes while the other extends) and the movement frequency is increased, the movement spontaneously switches to in-phase (both fingers flex and extend at the same time) at a certain critical rate . This does not mean that the subjects could not move their fingers faster, say due to biomechanical limitations, in fact they can but only in the in-phase pattern, not in anti-phase. Why is that so? As with most of the 'why' questions the answer is: we don't know. But then Sir Isaac Newton didn't know 'why' the apple falls or 'why' the moon moves around the earth, however he had figured out 'how'. So, how does coordination work and how can we describe or model its phenomena quantitatively?

In the early 1980s Scott Kelso met Hermann Haken, a theoretical physicist at the University of Stuttgart, Germany. Their collaboration led to a by now seminal paper in 1985, where they published what became known as the Haken-Kelso-Bunz or HKB model [7]. The model was worked out in the spirit of synergetics [6], a general theory for systems that are far from thermal equilibrium and undergo qualitative changes in their dynamical behavior (so-called *non-equilibrium phase transitions*) when an external quantity (the so-called *control parameter*) exceeds a critical threshold. Synergetics further predicts that even though the systems themselves are complex (in our case muscles, tendons, bones, joints, controlled by an even more complex system, the brain), close to transition points they exhibit low-dimensional behavior and their dynamics on a *macroscopic* scale can be described by a few collective variables, the so-called *order-parameters*. In systems from physics, like fluids or lasers, these order-parameters can be derived from a *mesoscopic* level where field theoretical equations, in fluid dynamics the Navier-Stokes equations, are known from basic laws of nature, here the conservation laws of energy and momentum. The strategy for modeling the transition from anti-phase to in-phase in human movement coordination had to be different as the laws guiding coordination- or brain dynamics on the mesoscopic level are not known a priori and cannot (yet?) be derived from basic principles. Therefore, the approach of Haken, Kelso and Bunz was top-down rather than bottom-up, i.e. to first find a description on the macroscopic, order-parameter level and then determine what kind of lower level dynamics can lead to such a macroscopic behavior.

2.1 The Macroscopic Level: Relative Phase

The first step in a top-down approach for movement coordination consists of determining one or a few quantities that represent the order-parameters together with a dynamical system for these variables which is consistent with the experimental observations, namely:

- At slow movement rates subjects can move their finger in either in-phase or anti-phase;
- If a movement is initially in anti-phase and the movement rate is increased subjects spontaneously switch to in-phase;
- If a movement is initially in in-phase and the movement rate is increased or decreased no transitions are observed.

Translated into the language of dynamical systems we can state: the movements of the single fingers are oscillations. Oscillations $x(t)$ are described by a closed trajectory (a limit cycle) in phase space with an amplitude $r(t)$ and a phase $\varphi(t)$. The difference between an in-phase and an anti-phase movement of two oscillators is captured by the the difference between their phases $\phi(t) = \varphi_1(t) - \varphi_2(t)$, the *relative phase*. Relative phase is 0 for an in-phase movement and π or 180° for an anti-phase movement and became the most important order-parameter of coordination dynamics.

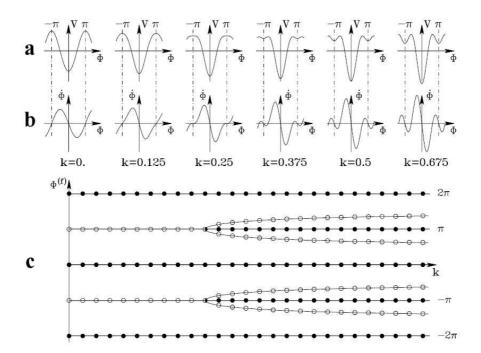Now we can reformulate the experimental findings above for the dynamics of the relative phase ϕ:

- At slow movement rates the dynamics for ϕ has two stable fixed points at $\phi = 0$ and $\phi = \pi$ and the system is bistable ;
- At fast rates there is only one stable fixed point at $\phi = 0$ and the system is monostable ;
- Relative phase is a cyclic quantity and its dynamics must be periodic modulo 2π, i.e. expressed in terms of sine and cosine functions.

The simplest dynamical system that fulfills all these requirements is given by

$$\dot{\phi} = -a \sin \phi - 2b \sin 2\phi \tag{1}$$

which can also be derived from a potential function

$$\dot{\phi} = -\frac{dV}{d\phi} \quad \text{with} \quad V = -a \cos \phi - b \cos 2\phi \tag{2}$$

Fig. 1. Dynamical properties of (1) as a function of the control parameter $k = b/a$. Potential function (a), phase space plot (b), and bifurcation diagram (c), where solid and open circles indicate branches of stable and unstable fixed points, respectively.

The control-parameter in this system is the ratio $k = \frac{b}{a}$ which corresponds to the movement rate. An increase in this ratio reflects a decrease in movement rate and vice versa. The critical value where anti-phase movement is no longer stable is given by $k = \frac{b}{a} = 0.25$. The dynamical properties of (1) are shown in Fig. 1 with the potential function in the top row (a), a phase space plot ($\dot{\phi}$ over ϕ) in the middle row (b), and a bifurcation diagram in the bottom row (c), where solid and open circles indicate branches of stable and unstable fixed points, respectively. A transition occurs when the system is started in anti-phase at values of k greater than 0.25 (corresponding to slow movements) and k is decreased to a value smaller than 0.25 (corresponding to an increase in movement rate beyond its critical value).

2.2 The Mesoscopic Level: Oscillators and their Coupling

As pointed out before, equation (1) describes coordination behavior on the macroscopic level of the quite abstract order-parameter relative phase. As shown already in the original HKB paper of 1985 [7] this equation can be derived from a lower level by modeling the oscillator dynamics of the moving fingers. In order to define a relative phase and derive (1), we need two oscillators and a coupling function. What would be a good oscillator to describe human limb movement? The easiest oscillating species, that is linear harmonic oscillators, are not good candidates because they do not have stable limit cycles. If a linear oscillation is perturbed, the system will switch to a new orbit. In contrast, if a human limb movement is perturbed, the oscillation will relax back to its original amplitude. We therefore need nonlinear terms in the oscillator equations and as it turns out the most important ones for our purpose are $x^2 \dot{x}$ (called a van-der-Pol term) and $\dot{x}^3$ (known as the Rayleigh term). Together this leads us to a system that has been termed hybrid oscillator and reads explicitly

$$\ddot{x} + \epsilon \dot{x} + \omega^2 x + \gamma x^2 \dot{x} + \delta \dot{x}^3 = 0 \qquad (3)$$

There are good reasons to pick this specific form. First there is symmetry. In human limb movements the flexion phase is in good approximation a mirror image of the extension phase. This means that the equation which describes such movements must be invariant if we substitute x by $-x$, reflecting a point symmetry with respect to the origin in phase space. This constraint does not allow any quadratic terms because they would violate the required invariance or break the symmetry. The second reason stems from two experimental findings. The amplitude of a moving limb decreases linearly with frequency as has been shown by Kay, Saltzman and Kelso [13] and the phase portraits of limb movements are almost circular.

To couple two oscillators of the form (3) such that their relative phase follows the dynamics described by (1) is the true challenge. We can think of coupled oscillators as two swinging pendulums connected by a spring. The force exerted by the spring onto the pendulums is then proportional to the

difference in their locations $x_1(t) - x_2(t)$. It is easy to show that such a coupling between two hybrid oscillators does not lead to a dynamics for the relative phase of the form (1). Closer investigation reveals that there are several ways that lead to the correct phase relation. The arguably easiest form of a coupling, which was also given in the original HKB paper, consists of a combination of differences in the locations and velocities of the individual components. In this case the complete system of coupled oscillators that leads to the phase relation (1) reads

$$\ddot{x}_1 + \epsilon \dot{x}_1 + \omega^2 x_1 + \gamma x_1^2 \dot{x}_1 + \delta \dot{x}_1^3 = (\dot{x}_1 - \dot{x}_2)\{\alpha + \beta(x_1 - x_2)^2\}$$
$$\ddot{x}_2 + \epsilon \dot{x}_2 + \omega^2 x_2 + \gamma x_2^2 \dot{x}_2 + \delta \dot{x}_2^3 = (\dot{x}_2 - \dot{x}_1)\{\alpha + \beta(x_2 - x_1)^2\}$$

(4)

The parameters a and b in (1) can now be expressed in terms of parameters in the oscillators and the coupling terms in (4) and read explicitly

$$a = -\alpha - 2\beta r^2 \qquad b = \frac{1}{2}\beta r^2 \quad \text{with} \quad r^2 = \frac{-\epsilon}{\gamma + 3\omega^2 \delta} \tag{5}$$

where r represents the amplitude and ω the frequency of the individual hybrid oscillators.

A numerical simulation of the system of coupled oscillators (4) is shown in Fig. 2. When the system is started in anti-phase and the frequency ω is continuously increased a switch to in-phase occurs at the critical value ω_c (top row). No transition occurs when the the oscillators are started in in-phase (bottom row).
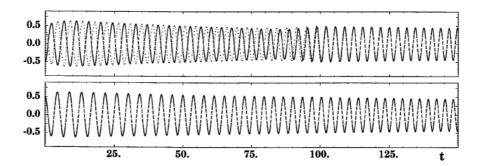

Fig. 2. Numerical simulations of (4) with initial conditions in anti-phase (top) and in-phase (bottom). The frequency is continuously increased from $\omega = 1.4$ on the left to $\omega = 2.1$ on the right. Switching at a critical value of ω_c occurs only in the anti-phase case (other parameters $\epsilon = -0.7$, $\gamma = \delta = 1$, $\alpha = -0.2$, $\beta = 0.5$).

It is important to be aware of the fact that there are other ways to introduce a coupling between two hybrid oscillators that leads to the right

dynamics for the relative phase. In general, the bottom-up approach from the mesoscopic to the macroscopic level of description of complex systems is unique, the top-down approach is not. However, knowledge of the macroscopic behavior of a system drastically reduces the possible models on the mesoscopic level and also provides important guidance for the design of experiments.

3 Breaking the Symmetry: $\Delta\omega$

The most striking feature of the Haken-Kelso-Bunz model is its validity when we go beyond the simple symmetric cases discussed above. What does the model predict when the two oscillators have different eigenfrequencies ω_1 and ω_2? In human movements such a scenario can be realized by coordinating an arm and a leg, for instance. If the eigenfrequencies are not too different the coupling between the oscillators will force them into 1:1 frequency locking . There are regions in parameter space where the coupled system can perform in-phase or anti-phase oscillations at a common frequency Ω. As before, starting from the system of coupled oscillators that corresponds to (4) but now with eigenfrequencies ω_1 and ω_2, the dynamics of the relative phase can be derived. As it turns out, the phase relation is the same as (1) with an additional constant on the right hand side commonly called the symmetry breaking term $\Delta\omega$, which can be expressed in terms of the two eigenfrequencies of the single oscillators ω_1 and ω_2 and the common frequency Ω of the coupled system

$$\dot{\phi} = \Delta\omega - a\sin\phi - 2b\sin 2\phi \qquad \text{with} \qquad \Delta\omega = \frac{\omega_1^2 - \omega_2^2}{\Omega} \approx \omega_1 - \omega_2 \qquad (6)$$

A finite value for the constant $\Delta\omega$ in (6) leads to qualitative changes in the dynamical behavior of the relative phase. First, the fixed points of (6) are not at $\phi = 0$ and $\phi = \pi$ anymore, but are given by the solution of the transcendental equation
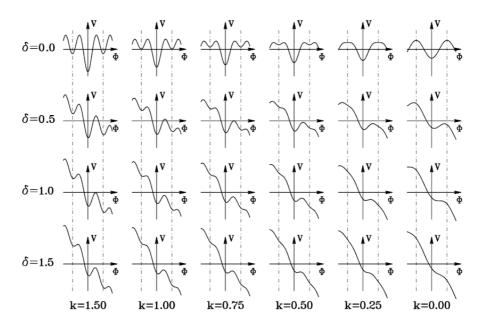
$$\Delta\omega - a\sin\phi - 2b\sin 2\phi = \Delta\omega - \sin\phi\{a - 4b\cos\phi\} = 0 \qquad (7)$$

For small values of $\Delta\omega$ these fixed points are shifted proportional to $\Delta\omega$ and can be written as

$$\phi^{(0)} = \frac{\Delta\omega}{a + 4b} \qquad \text{and} \qquad \phi^{(\pi)} = \pi - \frac{\Delta\omega}{a - 4b} \qquad (8)$$

The different eigenfrequencies not only lead to a shift of the fixed points, but also break the cyclic symmetry, i.e., the points $\phi = 0$ and $\phi = 2\pi$ are not the same anymore. The transitions that occur when the movement rate exceeds its critical value now have a preferred direction towards either 0 or 2π depending on the sign of $\Delta\omega$.

The potential as a function of k and $\Delta\omega$ is shown in Fig. 3. The symmetry breaking term leads to an additional slope in the HKB potential which destabilizes the fixed points at smaller k values as compared to the symmetric case.

Fig. 3. The potential as a function of $k = b/a$ and $\delta = \Delta\omega$.

With decreasing k and increasing $\Delta\omega$ first the fixed points at $\phi = \pm\pi$ disappear and finally also the fixed point at $\phi = 0$, which corresponds to in-phase movement, becomes unstable. At this point no fixed phase relation between the two oscillators exists anymore and a phenomenon known as *phase wrapping* occurs. Details of the behavior of relative phase are shown in Fig. 4 where ϕ is plotted as a function of time. $\Delta\omega$ is kept at 1.5 and k is decreased from an initial value of 1.5 by 0.1 at each of the vertical lines. First the systems settles in anti-phase but with decreasing k the fixed points drift away from $\phi = \pm\pi$. At a first critical value $k_c = 1$ the anti-phase movement becomes unstable and a switch to in-phase takes place. The new stable relative phase has shifted away from $\phi = 0$ and again shows a drift. As k decreases further a second critical value is reached where the in-phase movement becomes unstable and the relative phase starts wrapping. However, reminiscence of the in-phase fixed point can still be seen in this parameter region in form of a shallower slope around $\phi = 0$. As the movement rate increases further (with k decreasing) the curve develops more and more towards a straight line.

4 Beyond the HKB Model

Beyond the classic bimanual rhythmic coordination paradigm, Scott Kelso and his colleagues explored various extensions of this task. Or better: the bimanual
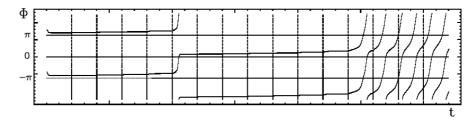
Fig. 4. Fixed point drift with decreasing k for a finite value of $\Delta\omega$. A switch from anti-phase to in-phase takes place at a first critical k_c and beyond a second critical value phase wrapping occurs.

coordination paradigm was used as an experimental window to address issues in learning, sensorimotor coordination, attention, and many other areas. Here we wish to illustrate two of these extensions.

4.1 On Sensorimotor Coordination

Experimental movement paradigms are very rarely independent of environmental influences. If they are, they are referred to as 'self-paced'. In most cases though, we deal with 'paced' movements, i.e. an external stimulus is delivered to the subject. This stimulus prescribes a pace at which the subjects should perform the finger movements. But in reality the stimulus does much more: it changes the stability and the variability of the relative phase of the movement; it also changes the variability of the target point (called anchoring) and the variability of the movement amplitude. In short, it couples the environment to the perception-action system. Kelso and colleagues investigated the role of environmental information in the dynamics of bimanual coordination. A central finding that emerged from this study was that external information may serve to stabilize states that would otherwise have switched to more stable modes of coordination. Jirsa et al. [8] accounted for this effect by coupling the external information parametrically to a set of limit cycle oscillators. The main idea elucidated by the above studies is that perception and action, environmental information and the dynamics of movement, are inextricably linked. This linkage, or coupling, has been shown to be of parametric nature (mathematically speaking: multiplicative coupling). In the following, we summarize the properties of this type of coupling and point to some of its implications.

The HKB model does not account for the presence of the metronome and in its original form can be described as a model for the intrinsic dynamics of the system. Recent experiments by Fink et al. [4] and Byblow et al. [3] have established that the metronome can modify the trajectories of movement. Further, Fink et al. demonstrated that the presence of the metronome causes not only local changes in the trajectory of movement but also introduces global effects to the dynamics, such as a shift of the critical frequency at

which a phase transition from the anti-phase to the in-phase mode of coordination takes place. In light of these experiments it becomes crucial to include the metronome into (4). The HKB model correctly reproduces a number of experimentally observed phenomena including phase transitions and hysteresis [7], critical fluctuations [16] and critical slowing down [22] among others. Hence, it is prudent to retain the HKB model at the core of other models that include environmental influences in a description of the dynamics of unimanual and bimanual coordination. For the latter, this was achieved by Schöner et al. [21] and Jirsa et al. [8]. Schöner et al. used an additive linear driving term to describe the effect of the metronome. The environmental information was introduced as an additional force acting on the order parameter dynamics attracting ϕ to the phase of the metronome. In contrast to account for the results of Fink, et al.'s recent experiments, Jirsa et al. used a parametric driving term to describe the effect of the metronome. In the limit of negligible coupling to the metronome both models reduce to the original HKB equations. Using equations of motion proposed by Jirsa et al., the coupling functions (right hand side of (4)) become

$$
\begin{aligned}
(\dot{x}_1 - \dot{x}_2)\{\alpha + \beta(x_1 - x_2)^2\} + \epsilon x_1 \cos \Omega t \\
(\dot{x}_2 - \dot{x}_1)\{\alpha + \beta(x_1 - x_2)^2\} + \epsilon x_2 \cos \Omega t
\end{aligned}
\tag{9}
$$

where the first terms denote the HKB coupling, Ω is the frequency at which the metronome is presented and ϵ is the strength of the parametric coupling.

In contrast to a linear driving or coupling, the multiplicative coupling can operate at multiple frequency ratios. In other words, such coupling allows for the stabilization of movement-stimulus frequency ratios 1:1, 1:2, 3:2, and others. Such is essential to allow for a maximum of flexibility for environment-subject (or agent) coupling and has been followed up by various other researchers [14, 2]. The multifrequency coupling regimes are illustrated in Fig. 5. In order to see frequency and phase locking in the experiment it is necessary that the Arnol'd tongue structures are wide enough so that the system does not fall into a qualitatively different solution due to small perturbations that are present in any biological system. The two broadest Arnol'd tongues correspond to the 1:1 and 1:2 modes of coordination and there are no other stable coordination modes in between.

Beyond flexibility in the frequency domain, multiplicative coupling also provides for a differential stabilization in the time domain. Such is clearly illustrated in Fig. 6, where phase flows obtained from computational simulations of the HKB model under parametric stimulation are shown. In particular, on the left, a situation is shown where only one stimulus per movement period is provided (single-metronome). Here the driving frequency is at the center of the 1:1 Arnol'd tongue (1.2 Hz). The points of peak flexion and extension are marked in the figure. Clearly, the trajectory shows lower variability at peak flexion in comparison to peak extension. This effect can be attributed to the presence of a stimulus at peak flexion which is absent at the opposite
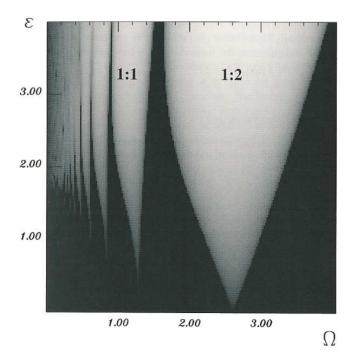
Fig. 5. Stability regions of parametric coupling are referred to as Arnol'd tongues and are plotted in light gray.

reversal point. On the right, the figure shows the effect of the stimulus on the trajectories of motion for the double metronome condition at a frequency at the center of the 1:2 Arnol'd tongue. Here, unlike in the previous case on the left of the figure, the trajectories are symmetric in phase space. In the double metronome condition, the environmental stimulus occurs at both peak flexion and peak extension. Hence, the trajectories at the two reversal points show similar variability. Figure 7 shows the corresponding situation for single- and double-metronome for real human data. Clearly, the same differences in the variability of the phase flows are observed, indicating differential stability in the time domain.

Despite the effect of *local* stabilization in the time domain, or better, in phase space, the following *global* consequence of multiplicative coupling is even more intriguing. It turns out that bimanual coordination under the double metronome stimulation is more stable than in the single metronome condition. This is reflected by a larger critical transition frequency and reduced variance of the relative phase between the left and right hand (and not between hand and stimulus!).We consider the coordination pattern of both hands (for instance, the in-phase or anti-phase pattern) as a global characteristic, since various information on both effector movements is needed, whereas a point
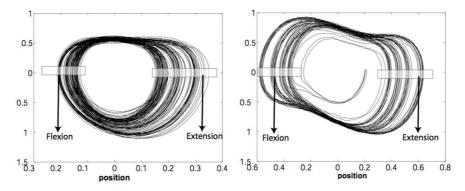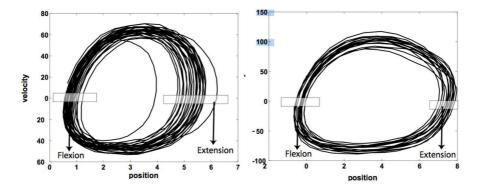
Fig. 6. Phase space trajectories when one stimulus (left) or two stimuli (right) are provided per movement cycle. Data are obtained from simulations.

Fig. 7. Experimentally obtained phase space trajectories when one stimulus (left) or two stimuli (right) are provided per movement cycle.

(and its trajectory variability) in the phase space of one effector (such as maximum flexion of the left hand) does not require this information. Hence, can we naively infer that additional information locally in the phase space stabilizes the global coordination pattern? Probably not. However, it seems safe to say that there exist local manipulations of phase space trajectories, which allow to control certain aspects of the entire movement system. Since a phase space trajectory is an entity which characterizes the dynamics of the movement, one could rephrase the former statement such as "if you know when and where to stimulate the end effector, then you control the whole system". The difficult part is the "where" and "when" for complex movements. For bimanual rhythmic coordination, Kelso and colleagues answered that question.

4.2 On Non-rhythmic Coordination

Often the question has been raised (repeatedly also by the current authors themselves), why are bimanual rhythmic movements interesting? The answer is that they are not, at least not from the perspective of real world applications. Per se these movements are quite limited. However, the bimanual rhythmic coordination paradigm has served as a beautiful entry point to probe the functioning of the nervous system. Still, this point taken, what do we learn about coordination in real world problems? In 2005, Jirsa and Kelso [12] extended the applicability of dynamic system theory to a wider range of movements, including discrete and continuous movements. The power of their approach lies in the generality of phase flows. All time-continuous and deterministic dynamics must be captured by the phase flows in phase space. Such is not just another model, but actually a theorem underlying the temporal evolution of dynamical systems. Furthermore, the topology of the phase flows qualifies as a candidate invariant as shown by various theorems in the theory of dynamical systems[1]. Hence, two dynamical systems (or in this context: movement systems) are different if, and only if, their phase space topologies are different. If the topologies are not different, then a transformation exists that allows to map one system upon the other. Hence, the systems are not really different. This insight provides us with a beautiful approach to classify human movements on the phenomenological level, i.e. without making reference to the underlying neural substrate. However, such shall not be the focus of our discussion here (instead, see Huys et al. (this volume) for a discussion of phase space topologies in the context of timing and Sternad (this volume) for a discussion of the discrete vs. rhythmic movement debate). Rather we assume the existence of phase flows (and leave it to the cited authors to dwell on these issues) and ask the question, how does the HKB paradigm contribute to the discrete-rhythmic movement debate? Or equivalently, does the HKB coupling extend to non-rhythmic movements and hence coordination? Kelso and colleagues [11, 12] went forward and addressed this question theoretically. First of all, rhythmic movements are limited to closed (in the ideal case circular) structures in phase space as illustrated in Fig. 8. The in-phase movement then corresponds to a motion where the coordinates (position u and velocity v) of both effectors (1 and 2) coincide (see lower row in Fig. 8) in phase space indicated here by x and y on the axes. The anti-phase movement corresponds to the situation when the two effectors assume the maximum distance in the alloted space (that is the circle) as shown in the upper row of Fig. 8.

Since these two states are both stable (flows convergent to the particular state) below a critical frequency, then, when following the line along the circle and separating the two effectors, (u, v), there must be a point where the flow

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[1] This statement is precise for two degrees of freedom. In higher dimensions, one may identify cases where the situation is less clear (such as low- or high-dimensional deterministic chaos). However, it is equally unclear and questionable if these special cases will ever be of any relevance for human movements.
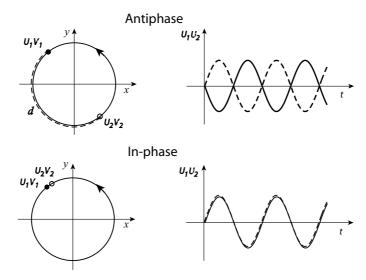
Fig. 8. Euclidean distance d of two limit cycle oscillators is maximal for anti-phase motion as a consequence of divergent dynamics and minimal for in-phase motion due to convergent dynamics.

switches its direction. This point on the circle identifies the maximum divergence in the coordination of the two effectors. If the HKB coupling is removed, the entire circle consists of neutral points only, that is the flow along the circle is zero, or put differently once again, any phase relation is allowed. Hence, Kelso and colleagues put forward that the nature and function of a coupling is to alter the existing flows in phase space in a meaningful manner [12]. This may be true for cognitive systems [11], but in particular for the movement system. If true, then such shall be true for arbitrary movements also (assuming that the nervous system does not adapt its couplings when switching from one movement type to another). Following this line of thought, Kelso and colleagues [12] implemented the HKB coupling in numerical simulations of arbitrary movements. The latter are characterized by not being constrained to the circle as in rhythmic movements (Fig. 8), but may explore a much larger phase space. The findings of these simulations are summarized in Fig. 9.

Essentially the convergence and divergence hypothesis translates to acceleration and deceleration phenomena of individual effectors in arbitrary but coordinated movement tasks. More specifically, when two discrete movements are executed bimanually (first with the one effector, then with the other) following two stimuli, then the movement time of the effectors will be influenced by the HKB coupling. Up to a certain maximal inter-stimulus interval (ISI) the two movement trajectories will converge in phase space. Beyond the critical ISI, the two movement trajectories will diverge. Translating this effect of convergence and divergence to more common measures in movement sciences,
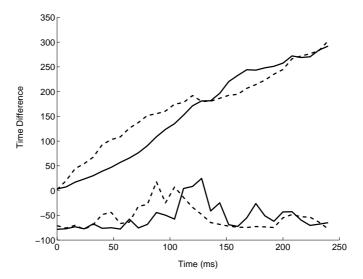
Fig. 9. Mean time difference of the two effectors (upper graphs) and its variance (lower graphs) are plotted as a function of the inter-stimulus interval. The time units are in msec. The dashed lines refer to the uncoupled situation, the solid lines to the coupled situation. The variance is not plotted on the same scale as the time difference graphs. The maximum variance is about 800msec^2 at an inter-stimulus interval of approximately 130msec.

we obtain the difference in movement time as illustrated in Fig. 9. This effect is a clear prediction – based upon the HKB coupling – within the domain of discrete movements and remains to be tested experimentally. In any case, the development of the convergence-divergence hypothesis of couplings illustrates beautifully how the HKB paradigm accomplishes in enriching other domains within movement sciences, which are at first sight beyond its reach.
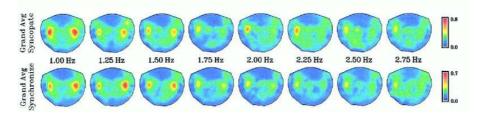
5 Neural Correlates of Coordination

Starting in the early 1990s a series of experiments have been conducted using noninvasive brain imaging techniques to identify the regions and networks in the brain that are activated when humans perform coordination tasks. Especially, the syncopation-synchronization paradigm (see below) has been studied using electroencephalography (EEG), magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI). These technologies are sensitive to different quantities and provide complementary aspects about information processing inside the brain. EEG and MEG reflect the electric neural activity with a high temporal resolution of milliseconds, whereas fMRI is a measure of the metabolism of cell clusters but provides true 3-dimensional information on a spatial scale of millimeters.

5.1 MEG

In several experiments MEG was used to record the magnetic field originating from neural activity while subjects performed coordination tasks [5, 17]. We will restrict ourselves here to results involving the *syncopation-synchronization paradigm* [15]. In this experimental setup a single limb (finger) is moved such that peek flexion occurs between the beats of an external metronome, i.e. in a syncopated fashion. When the metronome frequency is increased a critical value is reached where the subjects switch spontaneously to a movement where peek flexion occurs on the beat, i.e. in synchronization with the metronome.

While subjects performed the task, both their finger movements and neural activity was recorded. The movement profile was detected as pressure changes in a small air cushion connected to a transducer outside the magnetically shielded room that housed the MEG device. For brain recordings a fullhead magnetometer with about 150 SQuID (Superconducting Quantum Interference Device) sensors was used to measure the radial component of the magnetic field originating from tiny currents reflecting neural activity inside the brain.

Fig. 10. Global signal power changes from a bilateral pattern at low coordination rates to a pattern with only a single maximum over the contralateral hemisphere at fast rates. There is no significant difference between the conditions (note that at high rates the subjects have switched to synchronization).
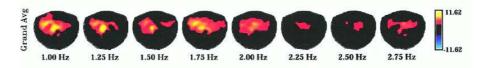

Fig. 11. Spatial distribution of activity synchronization minus syncopation in the β-band for different movement rates. All differences are positive, indicating a stronger β-desynchronization during syncopation. Interestingly, even after the switch to synchronization has occurred in the syncopation condition there is still a significant difference to β-activity when the initial coordination pattern was synchronization.
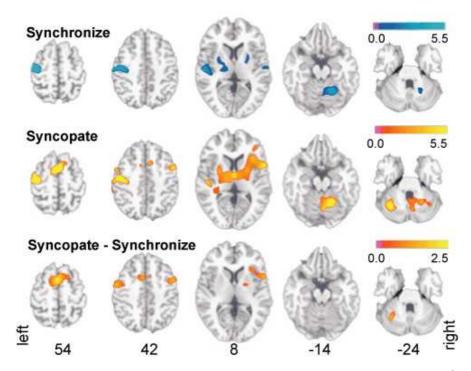
The main findings from these experiments include:

1. At low coordination rates the strongest signal power is found bilaterally in sensors over auditory and sensorimotor cortices. At high movement rates, where subjects can only synchronize, the activity over the ipsilateral hemisphere with respect to the finger movements disappears (Fig. 10).
2. In channels over the contralateral sensorimotor areas the spectrum component switches from the coordination frequency to its first harmonic [17].
3. The phase of the Fourier component corresponding to the coordination frequency in these channels undergoes a shift by 180° at the point where the movement undergoes its transition from anti-phase to in-phase.
4. The spatial pattern of the dominating mode from a principal component analysis corresponds to a pattern that reflects auditory activation for syncopation at low movement rates, whereas after the switch to synchronization the dominating pattern reflects sensorimotor activity.
5. The power in the β-band (15-30Hz) is significantly larger during synchronization compared to syncopation, or in other words, β-desynchronization is larger during syncopation than synchronization (Fig. 11).

5.2 fMRI

In recent years functional MRI has become widely available and the brain imaging technology of choice for many neuroscientists. The fMRI signal is based on the change in the magnetic properties of the hemoglobin molecules, the oxygen carrier in the blood. When oxygen is released to a cell oxyhemoglobin, which is diamagnetic, is transformed into deoxyhemoglobin, a paramagnetic molecule. The two forms interact differently with the spins in the regions where the oxygen release takes place, which leads to a detectable change in the magnetic resonance signal intensity. Therefore, fMRI is a not a direct measure of neural activity but of metabolism. Nevertheless, it provides a spatially high resolution real volume measure of the brain regions that are active when certain tasks are performed. This information complements the knowledge gained from technologies with high temporal resolution like MEG and EEG. Moreover, fMRI allows for detecting sub-cortical activity that cannot be picked up by the electrophysiological technologies.

Straightforward comparison of brain regions that are active when subjects performed syncopated and synchronized timing patterns revealed both similarities and differences [18]. When compared to rest, both coordination types trigged a larger fMRI signal in auditory cortices, the contralateral sensorimotor areas, the premotor and supplemental motor areas and the (primarily ipsilateral) cerebellum as shown in fig. 12. During syncopated movement, nevertheless, not only was activity in these brain regions increased as compared to synchronization, but also an additional network of areas including the basal ganglia, and prefrontal and temporal association cortices became active. Interestingly, there was not a single region where the activity during syncopation

Fig. 12. Active brain areas during synchronization (1st row), syncopation (2nd row) as well as the difference in activation between the two conditions (3rd row).

was smaller than in synchronization. When compared to a control condition where the subjects performed selfpaced movements at about the same rate activation in the cerebellum turned out to be increased for syncopation but decreased for synchronization.
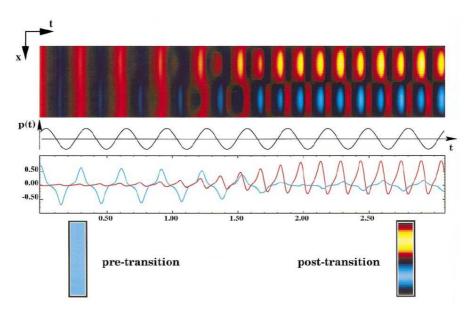
Taken together these results led to the conclusion that the synchronization timing pattern can be carried out relatively automatically as a sequence, whereas the syncopation pattern requires planning, initiating, monitoring and execution of each movement cycle individually.

5.3 Modeling of Neural Activity

The experimental findings from the MEG experiments summarized above were used by Jirsa and Haken [9, 10] to formulate a model of the underlying neural dynamics on a mesoscopic scale of the so-called neural field. Starting from the work of Wilson and Cowan [23, 24], and the wave equation approach by Nunez [19, 20] both dating back to the early 1970s, they derived an integral equation for the neural field $\psi(\mathbf{x}, t)$ on a cortical surface Γ which reads explicitly

$$\psi(\mathbf{x},t) = a\int_{\Gamma} d\mathbf{x}' f(\mathbf{x},\mathbf{x}')\, S\{\rho\,\psi(\mathbf{x}',t - \frac{|\mathbf{x}-\mathbf{x}'|}{v}) + p(\mathbf{x}',t - \frac{|\mathbf{x}-\mathbf{x}'|}{v})\}$$
$$(10)$$

Here $f(\mathbf{x},\mathbf{x}')$ represents the coupling between the locations $\mathbf{x}$ and $\mathbf{x}'$, p is an external input at location $\mathbf{x}'$ that affects the field at location $\mathbf{x}$ with a delay given by the distance $|\mathbf{x}-\mathbf{x}'|$ divided by the propagation velocity v. $S\{X\}$ is a sigmoidal function, and a and ρ are constants that represent synaptic weights and fiber density, respectively.

Fig. 13. Numerical simulation of (12). Top row: Space-time plot of the spatiotemporal activity. The dynamics undergoes a transition from a spatially homogenous oscillation pattern to an oscillation with a pattern that has a maximum and a minimum in space when the frequency of the external driving (2nd row) exceeds a critical value. 3rd row: Temporal amplitudes of the two dominating spatial patters (shown in the 4th row).

The form (10) is quite general in the sense that first the dimension of the cortical surface is not set and second the connectivity function $f(\mathbf{x},\mathbf{x}')$ is not explicitly defined, allowing both homogeneous connections between a location and its neighbors as well as heterogeneous connections realized as fiber bundles in the cortical white matter connecting distant brain regions. In the original work it was assumed that the cortical "surface" is one-dimensional, that there are no long-range or heterogenous connections in the system, and that the short-range homogenous connectivity between locations falls off exponentially with distance

$$f(x, x') = \frac{1}{2\sigma} e^{|x-x'|\sigma} \tag{11}$$

The latter is a good approximation for the short-range connectivity that is found experimentally in mammals [1].

Under these assumptions (10) can be written in form of a partial differential equation which is much easier to deal with than the retarded integral equation (10)

$$\ddot{\psi}(x,t) + (\omega_0^2 - v^2 \frac{\partial^2}{\partial x^2})\psi(x,t) + 2\omega_0 \dot{\psi}(x,t)$$
$$= a(\omega_0^2 + \omega_0 \frac{\partial}{\partial t})S\{\rho\,\psi(x,t) + p(x,t)\} \quad \text{with} \quad \omega_0 = \frac{v}{\sigma} \tag{12}$$

Results from a numerical simulation of (12) are shown in Fig. 13. The top row represents the spatio-temporal pattern of the one-dimensional neural sheet in a space-time plot. A qualitative change in the dynamical behavior from an oscillation of a spatially constant pattern to a pattern that has a maximum and minimum at each point in time is evident. The second row shows the external signal (metronome), driving the system with a constantly increasing frequency. The third row shows the amplitudes of a projection of the spatio-temporal signal onto the two patterns in the bottom row, also showing the transition in the dominating spatial pattern at the critical driving frequency. This simulation demonstrates that even with such a one-dimensional model the main experimental findings from the MEG experiments can be reproduced. Work on more realistic models using a two-dimensional surface and also heterogeneous long range connections between distant locations is currently under way.

6 Conclusion

From its beginning more than a quarter century ago coordination dynamics has come a long way. Not only has coordination behavior been modeled quantitatively, it is one of the few cases in the life sciences where such has been achieved for a system as complex as the human body. But the phenomena, in particular the transition phenomena that are studied in coordination dynamics, have also been used as a probe into the most complex system known to us, the human brain.

In this chapter we have summarized a small portion of the many contributions Scott Kelso has made to advance the science of coordination dynamics. We have done so from our point of view, which is the perspective of two theoretical physicists. What makes coordination dynamics fascinating to our species is the insight that it can be put on a solid quantitative foundation and that the same basic laws govern on all the levels covered in this volume: behavioral, neural or social dynamics.

In any case, the Irish man would be astounded of where Scott's finger wagging has led us to.

7 Acknowledgment

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