

## Movement Coordination

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### Glossary

- 18 **Control parameter** A parameter of internal or external  
 19 origin that when manipulated controls the system  
 20 in a nonspecific fashion and is capable of inducing  
 21 changes in the system's behavior. These changes may  
 22 be a smooth function of the control parameter, or  
 23 abrupt at certain critical values. The latter, also referred  
 24 to as phase transitions, are of main interest here as they  
 25 only occur in nonlinear systems and are accompanied  
 26 by phenomena like critical slowing down and fluctuation  
 27 enhancement that can be probed for experimentally.  
 28 **Haken–Kelso–Bunz (HKB) model** First published in  
 29 1985, the HKB model is the best known and probably  
 30 most extensively tested quantitative model in human  
 31 movement behavior. In its original form it describes  
 32 the dynamics of the relative phase between two oscillating  
 33 fingers or limbs under frequency scaling. The HKB model  
 34 can be derived from coupled nonlinear oscillators and has  
 35 been successfully extended in various ways, for instance,  
 36 to situations where different limbs like an arm and a leg,  
 37 a single limb and a metronome, or even two different  
 38 people are involved.  
 39 **Order parameter** Order parameters are quantities that  
 40 allow for a usually low-dimensional description of the  
 41 dynamical behavior of a high-dimensional system on a  
 42 macroscopic level. These quantities change their val-

ues abruptly when a system undergoes a phase transition. For example, density is an order parameter in the ice to water, or water to vapor transitions. In movement coordination the most-studied order parameter is relative phase, i. e. the difference in the phases between two or more oscillating entities.

**Phase transition** The best-known phase transitions are the changes from a solid to a fluid phase like ice to water, or from fluid to gas like water to vapor. These transitions are called first-order phase transitions as they involve latent heat, which means that a certain amount of energy has to be put into the system at the transition point that does not cause an increase in temperature. For the second-order phase transitions there is no latent heat involved. An example from physics is heating a magnet above its Curie temperature at which point it switches from a magnetic to a nonmagnetic state. The qualitative changes that are observed in many nonlinear dynamical systems when a parameter exceeds a certain threshold are also such second-order phase transitions.

### Definition of the Subject

Movement Coordination is present all the time in daily life but tends to be taken for granted when it works. One might say it is quite an **archaic** subject also for science. This changes drastically when some pieces of the locomotor system are not functioning properly because of injury, disease or age. In most cases it is only then that people become aware of the complex mechanisms that must be in place to control and coordinate the hundreds of muscles and joints in the body of humans or animals to allow for maintaining balance while maneuvering through rough terrains, for example. No robot performance comes even close in such a task.

Although these issues have been around for a long time it was only during the last quarter century that scientists developed quantitative models for movement coordination based on the theory of **nonlinear dynamical systems**. **Coordination dynamics**, as the field is now called, has become arguably the most developed and best tested quantitative theory in the life sciences.

More importantly, even though this theory was originally developed for modeling of bimanual finger movements, it has turned out to be universal in the sense that it is also valid to describe the **coordination patterns** observed between different limbs, like an arm and a leg, different joints within a single limb, like the wrist and elbow, and even between different people that perform movements while watching each other.

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## 95 Introduction

96 According to a dictionary definition: *Coordination* is the  
97 act of coordinating, making different people or things  
98 work together for a goal or effect.

99 When we think about *movement coordination* the  
100 “things” we make work together can be quite different like  
101 our legs for walking, fingers for playing the piano, mouth,  
102 tongue and lips for articulating speech, body expressions  
103 and the interplay between bodies in dancing and ballet,  
104 tactics and timing between players in team sports and so  
105 on, not to forget other advanced skill activities like skiing  
106 or golfing.

107 All these actions have one thing in common: they look  
108 extremely easy if performed by people who have learned  
109 and practiced these skills, and they are incredibly difficult  
110 for novices and beginners. Slight differences might exist  
111 regarding how these difficulties are perceived, for instance  
112 when asked whether they can play golf some people may  
113 say: “I don’t know, let me try”, and they expect to out-drive  
114 Tiger Woods right away; there are very few individuals  
115 with a similar attitude toward playing the piano.

116 The physics of golf as far as the ball and the club is  
117 concerned is almost trivial: hit the ball with the highest  
118 possible velocity with the club face square at impact, and  
119 it will go straight and far. The more tricky question is  
120 how to achieve this goal with a body that consists of hun-  
121 dreds of different muscles, tendons and joints, and, im-  
122 portantly, their sensory support in joint, skin and muscle  
123 **support** (proprioception), in short, hundreds of **degrees**  
124 **of freedom**. How do these individual elements work to-  
125 gether, how are they coordinated? Notice, the question is  
126 not how do *we* coordinate them? None of the skills men-  
127 tioned above can be performed by consciously controlling  
128 all the body parts involved. Conscious thinking sometimes  
129 seems to do more harm than good. So how do they/*we*  
130 do it? For some time many scientists sought the answer to  
131 this question in what is called **motor programs** or, more re-  
132 cently, **internal models**. The basic idea is straightforward:  
133 when a skill is learned it is somehow stored in the brain  
134 like a program in a computer and simply can be called  
135 and executed when needed. Additional learning or train-  
136 ing leads to skill improvement, interpreted as refinements  
137 in the program. As intuitive as this sounds and even if one  
138 simply ignores all the unresolved issues like how such pro-  
139 grams gain the necessary flexibility or in what form they  
140 might be stored in the first place, there are even deeper rea-  
141 sons and arguments suggesting that humans (or animals  
142 for that matter) don’t work like that. One of the most strik-  
143 ing of these arguments is known as **motor equivalence**: ev-  
144 erybody who has learned to write with one of their hands

145 can immediately write with the foot as well. This writing  
146 may not look too neat, but it will certainly be readable  
147 and represents the transfer of a quite complex and diffi-  
148 cult movement from one end-effector (the hand) to an-  
149 other (the foot) that is controlled by a completely different  
150 set of muscles and joints. Different degrees of freedom and  
151 redundancy in the joints can still produce the same output  
152 (the letters) immediately, i. e. without any practice.

153 For the study of movement coordination a most im-  
154 portant entry point is to look at situations where the move-  
155 ment or coordination pattern changes abruptly. An exam-  
156 ple might be the well-known gait switches from walk to  
157 trot to gallop that horses perform. It turns out, however,  
158 that switching among patterns of coordination is a ubiq-  
159 uitous phenomenon in human limb movements. As will  
160 be described in detail, such switching has been used to  
161 probe human movement coordination in quantitative ex-  
162 periments.

163 It is the aim of this article to describe an approach to  
164 a **quantitative modeling** of human movements, called co-  
165 ordination dynamics, that deals with quantities that are ac-  
166 cessible from experiments and makes predictions that can  
167 and have been tested. The intent is to show that coordi-  
168 nation dynamics represents a theory allowing for quanti-  
169 tative predictions of phenomena in a way that is unprece-  
170 dented in the life sciences. In parallel with the rapid de-  
171 velopment of noninvasive brain imaging techniques, co-  
172 ordination dynamics has even pointed to new ways for the  
173 study of brain functioning.

## The Basic Law of Coordination: Relative Phase 174

175 The basic experiment, introduced by one of us [27,28], that  
176 gave birth to coordination dynamics, the theory underly-  
177 ing the coordination of movements, is easily demonstrated  
178 and has become a classroom exercise for generations of  
179 students: if a subject is moving the two index fingers in so-  
180 called **anti-phase**, i. e. one finger is flexing while the other is  
181 extending, and then the movement rate is increased, there  
182 is a **critical rate** where the subject switches spontaneously  
183 from the anti-phase movement to **in-phase**, i. e. both fin-  
184 gers are now flexing and extending at the same time. On  
185 the other hand, if the subject starts at a high or low rate  
186 with an in-phase movement and the rate is slowed down  
187 or sped up, no such transition occurs.

188 These experimental findings can be translated or  
189 mapped into the language of dynamical systems theory as  
190 follows [19]:

- 191 • At low movement rates the system has two **stable at-**  
192 **tractors**, one representing anti-phase and one for in-  
193 phase – in short: the system is **bistable**;

- 194 • When the movement rate reaches a critical value, the  
195 anti-phase attractor disappears and the only possible  
196 stable movement pattern remaining is in-phase;
- 197 • There is strong **hysteresis**, when the system is perform-  
198 ing in-phase and the movement rate is decreased from  
199 a high value, the anti-phase attractor may reappear but  
200 the system does not switch to it.

201 In order to make use of dynamical systems theory for  
202 a quantitative description of the transitions in coordinated  
203 movements, one needs to establish a measure that allows  
204 for a formulation of a dynamical system that captures  
205 these experimental observations and can serve as a phe-  
206 nomenological model. Essentially, the finger movements  
207 represent oscillations (as will be discussed in more detail  
208 in Subsect. “Oscillators for Limb Movements”) each of  
209 which is described by an amplitude  $r$  and a phase  $\varphi(t)$ . For  
210 the easiest case of harmonic oscillations the amplitude  $r$   
211 does not depend on time and the phase increases linearly  
212 with time at a constant rate  $\omega$ , called the angular velocity,  
213 leading to  $\varphi(t) = \omega t$ . Two oscillators are said to be  
214 in the in-phase mode if the two phases are the same, or  
215  $\varphi_1(t) - \varphi_2(t) = 0$ , and in anti-phase if the difference between  
216 their two phases is  $180^\circ$  or  $\pi$  radians. Therefore, the  
217 quantity that is most commonly used to model the exper-  
218 imental findings in movement coordination is the phase  
219 difference or **relative phase**

$$\phi(t) = \varphi_1(t) - \varphi_2(t) = \begin{cases} \phi(t) = 0 & \text{for in-phase} \\ \phi(t) = \pi & \text{for anti-phase} \end{cases} \quad (1)$$

221 The minimal dynamical system for the relative phase  
222 that is consistent with observations is known as the  
223 **Haken-Kelso-Bunz (or HKB) model** and was first pub-  
224 lished in a seminal paper in 1985 [19]

$$\dot{\phi} = -a \sin \phi - 2b \sin 2\phi \quad \text{with} \quad a, b \geq 0. \quad (2)$$

226 As is the case for all one-dimensional first order differen-  
227 tial equations, (2) can be derived from a **potential function**

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

229 One of the two parameters  $a$  and  $b$  that appear in (2)  
230 and (3) can be eliminated by introducing a new time scale  
231  $\tau = \alpha t$ , a procedure known as scaling and commonly used  
232 within the theory of nonlinear differential equations, lead-

ing to

$$\begin{aligned} \dot{\phi}(t) &= \frac{d\phi(t)}{dt} \rightarrow \frac{d\phi\left(\frac{\tau}{\alpha}\right)}{d\frac{\tau}{\alpha}} \\ &= -a \sin \phi\left(\frac{\tau}{\alpha}\right) - 2b \sin 2\phi\left(\frac{\tau}{\alpha}\right) \quad (4) \\ \alpha \frac{d\tilde{\phi}(\tau)}{d\tau} &= -a \sin \tilde{\phi}(\tau) - 2b \sin 2\tilde{\phi}(\tau) \end{aligned}$$

where  $\tilde{\phi}$  has the same shape as  $\phi$ , it is just changing on  
a slower or faster time scale depending on whether  $\alpha$  is  
bigger or smaller than 1. After dividing by  $\alpha$  and letting  
the so far undetermined  $\alpha = a$  (4) becomes

$$\frac{d\tilde{\phi}}{d\tau} = -\underbrace{\frac{a}{\alpha}}_{=1} \sin \tilde{\phi} - 2 \underbrace{\frac{b}{\alpha}}_{=k} \sin 2\tilde{\phi}. \quad (5)$$

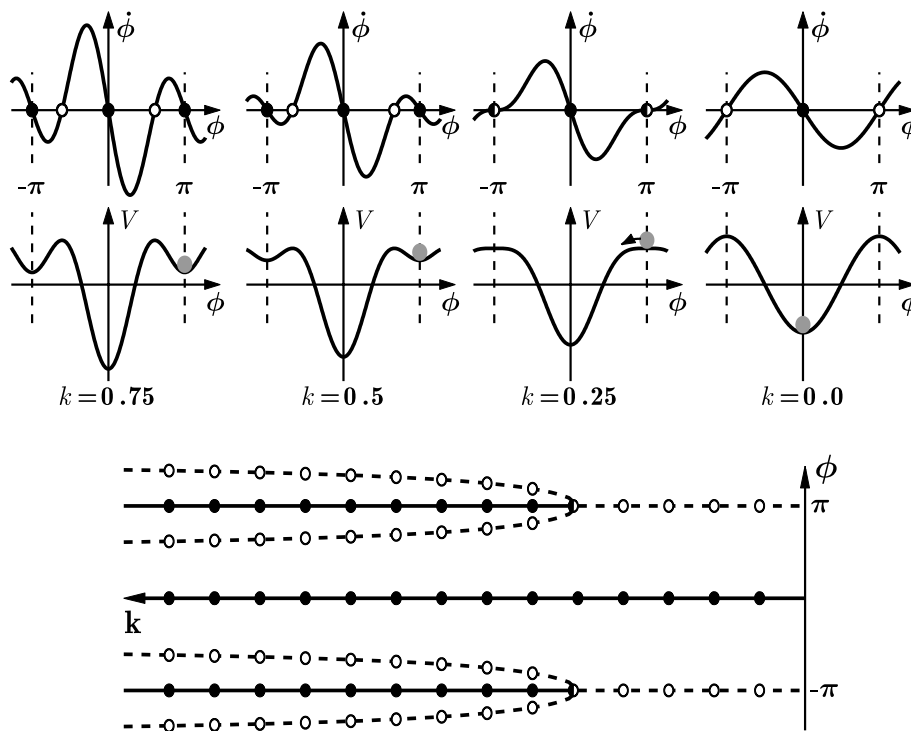
Finally, by dropping the tilde (2) and (3) can be written  
with only one parameter  $k = \frac{b}{a}$  in the form

$$\begin{aligned} \dot{\phi} &= -\sin \phi - 2k \sin 2\phi \\ &= -\frac{dV(\phi)}{d\phi} \quad \text{with} \quad V(\phi) = -\cos \phi - k \cos 2\phi. \quad (6) \end{aligned}$$

The dynamical properties of the HKB model’s **collec-  
tive** or **coordinative level of description** are visualized in  
Fig. 1 with plots of the phase space ( $\dot{\phi}$  as a function of  $\phi$ )  
in the top row, the potential landscapes  $V(\phi)$  in the second  
row and the **bifurcation diagram** at the bottom. The control  
parameter  $k$ , as shown, is the ratio between  $b$  and  $a$ ,  
 $k = \frac{b}{a}$ , which is inversely related to the movement rate:  
a large value of  $k$  corresponds to a slow rate, whereas  $k$   
close to zero indicates that the movement rate is high.

In the phase space plots (Fig. 1 top row) for  $k = 0.75$   
and  $k = 0.5$  there exist two stable fixed points at  $\phi = 0$   
and  $\phi = \pi$  where the function crosses the horizontal axis  
with a negative slope, marked by solid circles (the fixed  
point at  $-\pi$  is the same as the point at  $\pi$  as the function is  
 $2\pi$ -periodic). These **attractors** are separated by **repellers**,  
zero crossings with a positive slope and marked by open  
circles. For the movement rates corresponding to these  
two values of  $k$  the model suggests that both anti-phase  
and in-phase movements are stable. When the rate is in-  
creased, corresponding to a decrease in the control param-  
eter  $k$  down to the critical point at  $k_c = 0.25$  the former  
stable fixed point at  $\phi = \pi$  collides with the unstable fixed  
point and becomes neutrally stable indicated by a half-  
filled circle. Beyond  $k_c$ , i. e. for faster rates and smaller val-  
ues of  $k$  the anti-phase movement is unstable and the only  
remaining stable coordination pattern is in-phase.

The potential functions, shown in the second row in  
Fig. 1, contain the same information as the phase space



**Movement Coordination, Figure 1**

Dynamics of the HKB model at the coordinative, relative phase ( $\phi$ ) level as a function of the control parameter  $k = \frac{b}{a}$ . *Top row:* Phase space plots  $\dot{\phi}$  as a function of  $\phi$ . *Middle:* Landscapes of the potential function  $V(\phi)$ . *Bottom:* Bifurcation diagram, where *solid lines with filled circles* correspond to stable fixed points (attractors) and *dashed lines with open circles* denote repellers. Note that  $k$  increases from right ( $k = 0$ ) to left ( $k = 0.75$ )

271 portraits as they are just a different representation of the  
 272 dynamics. However, the strong hysteresis is more intuitive  
 273 in the potential landscape than in phase space, and can  
 274 best be seen through an experiment that starts out with  
 275 slow movements in anti-phase (indicated by the gray ball  
 276 in the minimum of the potential at  $\phi = \pi$ ) and increasing  
 277 rate. After passing the **critical value**  $k_c = 0.25$  the slight-  
 278 est perturbation will put the ball on the downhill slope  
 279 and initiate a switch to in-phase. If the movement is now  
 280 slowed down again, going from right to left in the plots,  
 281 even though the minimum at  $\phi = \pi$  reappears, the ball  
 282 cannot jump up and occupy it but will stay in the deep  
 283 minimum at  $\phi = 0$ .

284 Finally, a bifurcation diagram is shown at the bottom  
 285 of Fig. 1, where the locations of stable fixed points for the  
 286 relative phase  $\phi$  are plotted as solid lines with solid circles  
 287 and unstable fixed points as dashed lines with open circles.  
 288 Around  $k_c = 0.25$  the system undergoes a subcritical  
 289 **pitchfork bifurcation**. Note that the control parameter  $k$  in  
 290 this plot increases from right to left.

291 Evidently, the dynamical system represented by (2) is  
 292 capable of reproducing the basic experimental findings

293 listed above. From the viewpoint of theory, this is simply  
 294 one of the preliminaries for a model that have to be ful-  
 295 filled. In general, any model that only reproduces what is  
 296 built into it is not of much value. More important are crucial  
 297 experimental tests of the consequences and additional  
 298 phenomena that are predicted when the model is worked  
 299 through. Several such consequences and predictions will  
 300 be described in detail in the following sections. It is only  
 301 after such theoretical and experimental scrutiny that the  
 302 HKB model has come to qualify as an elementary law of  
 303 movement coordination.

**Stability: Perturbations and Fluctuations**

304 Random fluctuations, or noise for short, exist in all sys-  
 305 tems that dissipate energy. In fact, there exists a famous  
 306 theorem that goes back to Einstein, known as the dissipa-  
 307 tion-fluctuation theorem, which states that the amount of  
 308 random fluctuations in a system is proportional to its dis-  
 309 sipation of energy. There are effects from **random noise** on  
 310 the dynamics of relative phase that can be predicted from  
 311 theory both qualitatively and quantitatively, allowing for  
 312

the HKB model's coordination level to be tested experimentally. Later the individual component level will be discussed.

An essential difference between the dynamical systems approach to movement coordination and the motor program or internal model hypotheses is most distinct in regions where the coordination pattern undergoes a spontaneous qualitative change as in the switch from anti-phase to in-phase in Kelso's experiment. From the latter point of view, these switches simply happen, very much like in the automatic transmission of a car: whenever certain criteria are fulfilled, the transmission switches from one gear to another. It is easy to imagine a similar mechanism to be at work and in control of the transitions in movements: as soon as a certain rate is exceeded, the anti-phase program is somehow replaced by the in-phase module, which is about all we can say regarding the mechanism of switching. On the other hand, by taking dynamic systems theory seriously, one can predict and test phenomena accompanying second-order phase transitions. Three of these phenomena, namely, critical slowing down, enhancement of fluctuations and critical fluctuations will be discussed here in detail.

For a quantitative treatment it is advantageous to expand  $\dot{\phi}$  and  $V(\phi)$  in (6) into Taylor series around the fixed point  $\phi = \pi$  and truncate them after the linear and quadratic terms, respectively

$$\begin{aligned}\dot{\phi} &= -\sin \phi - 2k \sin 2\phi \\ &= -\{-(\phi - \pi) + \dots\} - 2k\{2(\phi - \pi) + \dots\} \\ &\approx (1 - 4k)(\phi - \pi) \\ V(\phi) &= -\cos \phi - k \cos 2\phi \\ &= -\{-1 + (\phi - \pi)^2 + \dots\} \\ &\quad - k\{1 - 4(\phi - \pi)^2 + \dots\} \\ &\approx 1 - k - (1 - 4k)(\phi - \pi)^2.\end{aligned}\tag{7}$$

A typical situation that occurs when a system approaches and passes through a transition point is shown in Fig. 2. In the top row the potential function for  $\phi \geq 0$  is plotted (dashed line) together with its expansion around the fixed point  $\phi = \pi$  (solid). The bottom row consists of plots of time series showing how the fixed point is or is not approached when the system is initially at  $\phi = \pi + \Delta$ . The phenomena accompanying second-order phase transitions in a system that contains random fluctuations can be best described by Fig. 2.

**Critical slowing down** corresponds to the time it takes the system to recover from a small perturbation  $\Delta$ . In the vicinity of the fixed point the dynamics can be described by the linearization of the nonlinear equation

around the fixed point (7). Such a linear equation can be readily solved leading to

$$\phi(t) = \pi + \Delta e^{(1-4k)t}.$$

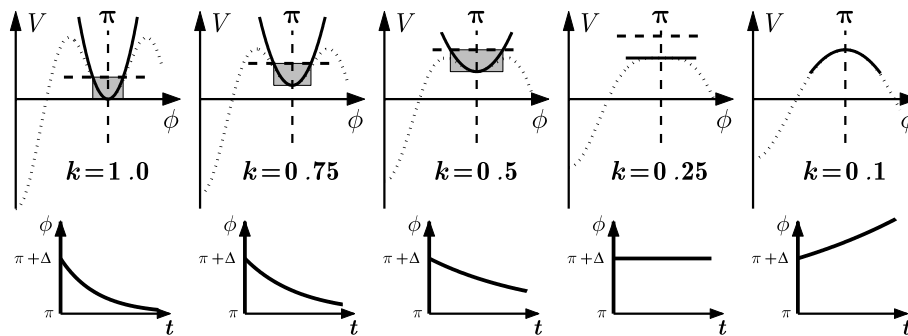
As long as  $k$  is larger than its critical value  $k_c = 0.25$  the exponent is negative and a perturbation will decay exponentially in time. However, as the system approaches the transition point, this decay will take longer and longer as shown in the bottom row in Fig. 2. At the critical parameter  $k = 0.25$  the system will no longer return to the former stable fixed point and beyond that value it will even move away from it. In the latter parameter region the linear approximation is no longer valid. Critical slowing down can be and has been tested experimentally by perturbing a coordination state and measuring the relaxation constant as a function of movement rate prior to the transition. The experimental findings [31,44,45] are in remarkable agreement with the theoretical predictions of coordination dynamics.

**Enhancement of fluctuations** is to some extent the stochastic analog to critical slowing down. The random fluctuations that exist in all dissipative systems are a stochastic force that kicks the system away from the minimum and (on average) up to a certain elevation in the potential landscape, indicated by the shaded areas in Fig. 2. For large values of  $k$  the horizontal extent of this area is small but becomes larger and larger when the transition point is approached. Assuming that the strength of the random force does not change with the control parameter, the standard deviation of the relative phase is a direct measure of this enhancement of fluctuations and will be increasing when the control parameter is moving towards its critical value. Again experimental tests are in detailed agreement with the stochastic version of the HKB model [30,44].

**Critical fluctuations** can induce transitions even when the critical value of the control parameter has not been reached. As before, random forces will kick the system around the potential minimum and up to (on average) a certain elevation. If this height is larger than the hump it has to cross, as is the case illustrated in Fig. 2 for  $k = 0.5$ , a transition will occur, even though the fixed point is still classified as stable. In excellent agreement with theory, such critical fluctuations were observed in the original experiments by Kelso and colleagues and have been found in a number of related experimental systems [31,42].

All these hallmarks point to the conclusion that transitions in movement coordination are not simply a switch-

**CE2** Is my change here ok?



Movement Coordination, Figure 2

Hallmarks of a system that approaches a transition point: enhancement of fluctuations, indicated by the increasing size of the shaded area; critical slowing down shown by the time it takes for the system to recover from a perturbation (bottom); critical fluctuations occur where the top of the shaded area is higher than the closest maximum in the potential, initiating a switch even though the system is still stable

ing of gears but take place in a well defined way via the instability of a former stable coordination state. Such phenomena are also observed in systems in physics and other disciplines where in situations far from thermal equilibrium macroscopic patterns emerge or change, a process termed self-organization. A general theory of self-organizing systems, called synergetics [17,18], was formulated by Hermann Haken in the early 1970s.

### The Oscillator Level

The foregoing description and analysis of bimanual movement coordination takes place on the coordinative or collective level of relative phase. Looking at an actual experiment, there are two fingers moving back and forth and one may ask whether it is possible to find a model on the level of the oscillatory components from which the dynamics of the relative phase can then be derived. The challenge for such an endeavor is at least twofold: first, one needs a dynamical system that accurately describes the movements of the individual oscillatory components (the fingers). Second, one must find a coupling function for these components that leads to the correct relation for the relative phase (2).

### Oscillators for Limb Movements

In terms of oscillators there is quite a variety to choose from as most second order systems of the form

$$\ddot{x} + \gamma \dot{x} + \omega^2 x + N(x, \dot{x}) = 0 \tag{8}$$

are potential candidates. Here  $\omega$  is the angular frequency,  $\gamma$  the linear damping constant and  $N(x, \dot{x})$  is a function containing nonlinear terms in  $x$  and  $\dot{x}$ .

Best known and most widely used are the harmonic oscillators, where  $N(x, \dot{x}) = 0$ , in particular for the case without damping  $\gamma = 0$ . In the search for a model to describe human limb movements, however, harmonic oscillators are not well suited, because they do not have stable limit cycles. The phase space portrait of an harmonic oscillator is a circle (or ellipse), but only if it is not perturbed. If such a system is slightly kicked off the trajectory it is moving on, it will not return to its original circle but continue to move on a different orbit. In contrast, it is well known that if a rhythmic human limb movement is perturbed, this perturbation decreases exponentially in time and the movement returns to its original trajectory, a stable limit cycle, which is an object that exists only for nonlinear oscillators [26,45].

Obviously, the amount of possible nonlinear terms to choose from is infinite and at first sight, the task to find the appropriate ones is like looking for a needle in a haystack. However, there are powerful arguments that can be made from both, theoretical reasoning and experimental findings, that restrict the nonlinearities, as we shall see, to only two. First, we assume that the function  $N(x, \dot{x})$  takes the form of a polynomial in  $x$  and  $\dot{x}$  and that this polynomial is of the lowest possible order. So the first choice would be to assume that  $N$  is quadratic in  $x$  and  $\dot{x}$  leading to an oscillator of the form

$$\ddot{x} + \gamma \dot{x} + \omega^2 x + ax^2 + b\dot{x}^2 + cx\dot{x} = 0. \tag{9}$$

How do we decide whether (9) is a good model for rhythmic finger movements? If a finger is moved back and forth, that is, performs an alternation between flexion and extension, then this process is to a good approximation symmetric: flexion is the mirror image of extension. In the equations a mirror operation is carried out by substituting  $x$

466 by  $-x$ , and, in doing so, the equation of motion must not  
 467 change for symmetry to be preserved. Applied to (9) this  
 468 leads to

$$\begin{aligned}
 & -\ddot{x} + \gamma(-\dot{x}) + \omega^2(-x) + a(-x)^2 + b(-\dot{x})^2 \\
 & + c(-x)(-\dot{x}) = 0 \\
 & -\ddot{x} - \gamma\dot{x} - \omega^2x + ax^2 + b\dot{x}^2 + cx\dot{x} = 0 \quad (10) \\
 & \ddot{x} + \gamma\dot{x} + \omega^2x - ax^2 - b\dot{x}^2 - cx\dot{x} = 0
 \end{aligned}$$

470 where the last equation in (10) is obtained by multiplying  
 471 the second equation by  $-1$ . It is evident that this equa-  
 472 tion is not the same as (9). In fact, it is only the same if  
 473  $a = b = c = 0$ , which means that there must not be any  
 474 quadratic terms in the oscillator equation if one wants  
 475 to preserve the symmetry between flexion and extension  
 476 phases of movement. The argument goes even further:  
 477  $N(x, \dot{x})$  must not contain any terms of even order in  $x$  and  
 478  $\dot{x}$  as all of them, like the quadratic ones, would break the  
 479 required symmetry. It is easy to convince oneself that as  
 480 far as the **flexion-extension symmetry** is concerned all odd  
 481 terms in  $x$  and  $\dot{x}$  are fine.

482 There are four possible cubic terms, namely  $\dot{x}^3$ ,  $\dot{x}x^2$ ,  
 483  $x\dot{x}^2$  and  $x^3$  leading to a general oscillator equation of the  
 484 form

$$\ddot{x} + \gamma\dot{x} + \omega^2x + \delta\dot{x}^3 + \epsilon\dot{x}x^2 + ax^3 + bx\dot{x}^2 = 0. \quad (11)$$

485 The effects that these nonlinear terms exert on the oscilla-  
 486 tor dynamics can be best seen by rewriting (11) as

$$\ddot{x} + \dot{x} \underbrace{\{\gamma + \epsilon x^2 + \delta \dot{x}^2\}}_{\text{damping}} + x \underbrace{\{\omega^2 + ax^2 + b\dot{x}^2\}}_{\text{frequency}} = 0 \quad (12)$$

489 which shows that the terms  $\dot{x}^3$  and  $\dot{x}x^2$  are position and  
 490 velocity dependent changes to the damping constant  $\gamma$ ,  
 491 whereas the nonlinearities  $x^3$  and  $x\dot{x}^2$  mainly influence the  
 492 frequency. As the nonlinear terms were introduced to ob-  
 493 tain stable limit cycles and the main interest is in ampli-  
 494 tude and not frequency, we will let  $a = b = 0$ , which re-  
 495 duces the candidate oscillators to

$$\ddot{x} + \dot{x}\{\gamma + \epsilon x^2 + \delta \dot{x}^2\} + \omega^2x = 0. \quad (13)$$

497 Nonlinear oscillators with either  $\delta = 0$  or  $\epsilon = 0$  have been  
 498 studied for a long time and have been termed in the litera-  
 499 ture as van-der-Pol and Rayleigh oscillator, respectively.

500 Systems of the form (13) only show sustained oscilla-  
 501 tions on a stable limit cycle within certain ranges of the  
 502 parameters, as can be seen easily for the **van-der-Pol oscil-**  
 503 **lator**, given by (13) with  $\delta = 0$

$$\ddot{x} + \dot{x} \underbrace{\{\gamma + \epsilon x^2\}}_{\tilde{\gamma}} + \omega^2x = 0. \quad (14)$$

The underbraced term in (14) represents the effective  
 damping constant,  $\tilde{\gamma}$ , now depending on the square of the  
 displacement,  $x^2$ , a quantity which is non-negative. For the  
 parameters  $\gamma$  and  $\epsilon$  one can distinguish the following four  
 cases:

505  $\gamma > 0, \epsilon > 0$  The effective damping  $\tilde{\gamma}$  is always positive. 510  
 506 The trajectories are evolving towards the origin, which 511  
 507 is a stable fixed point. 512

513  $\gamma < 0, \epsilon < 0$  The effective damping  $\tilde{\gamma}$  is always negative. 513  
 514 The system is unstable and the trajectories are evolving 514  
 515 towards infinity. 515

516  $\gamma > 0, \epsilon < 0$  For small values of the amplitude  $x^2$  the ef- 516  
 517 fective damping  $\tilde{\gamma}$  is positive leading to even smaller 517  
 518 amplitudes. For large values of  $x^2$  the effective damp- 518  
 519 ing  $\tilde{\gamma}$  is negative leading to a further increase in ampli- 519  
 520 tude. The system evolves either towards the fixed point 520  
 521 or towards infinity depending on the initial conditions. 521

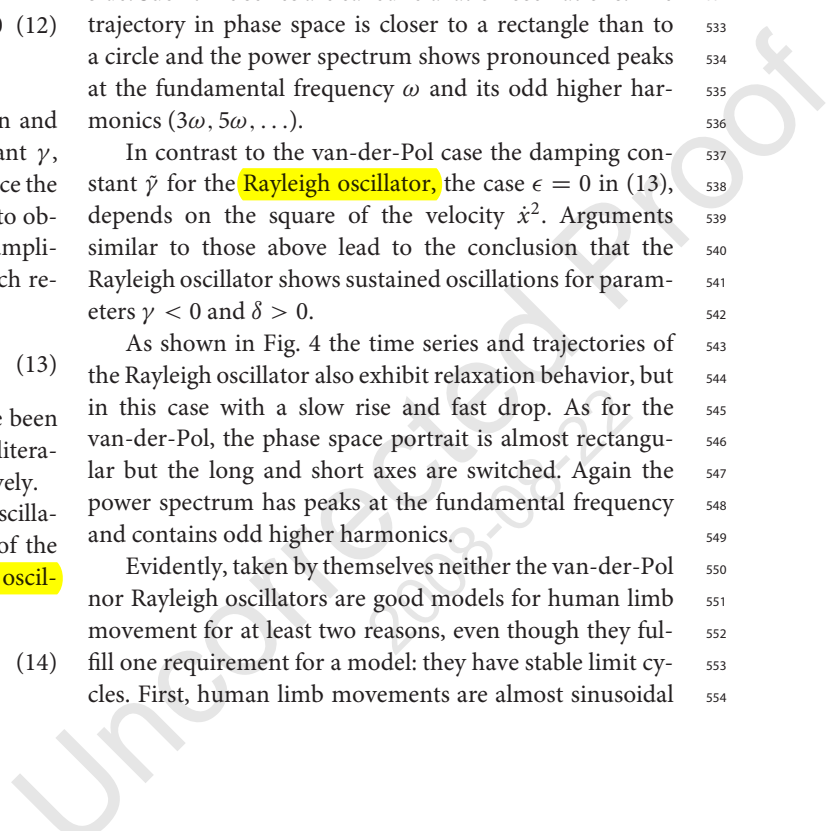
522  $\gamma < 0, \epsilon > 0$  For small values of the amplitude  $x^2$  the ef- 522  
 523 fective damping  $\tilde{\gamma}$  is negative leading to an increase in 523  
 524 amplitude. For large values of  $x^2$  the effective damping 524  
 525  $\tilde{\gamma}$  is positive and decreases the amplitude. The system 525  
 526 evolves towards a stable limit cycle. 526

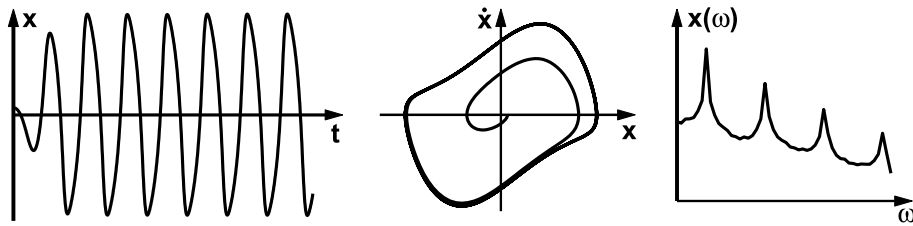
527 The main features for the van-der-Pol oscillator are 527  
 528 shown in Fig. 3 with the time series (left), the phase space 528  
 529 portrait (middle) and the power spectrum (right). The 529  
 530 time series is not a sine function but has a fast rising in- 530  
 531 creasing flank and a more shallow slope on the decreasing 531  
 532 side. Such time series are called relaxation oscillations. The 532  
 533 trajectory in phase space is closer to a rectangle than to 533  
 534 a circle and the power spectrum shows pronounced peaks 534  
 535 at the fundamental frequency  $\omega$  and its odd higher har- 535  
 536 monics ( $3\omega, 5\omega, \dots$ ). 536

537 In contrast to the van-der-Pol case the damping con- 537  
 538 stant  $\tilde{\gamma}$  for the **Rayleigh oscillator**, the case  $\epsilon = 0$  in (13), 538  
 539 depends on the square of the velocity  $\dot{x}^2$ . Arguments 539  
 540 similar to those above lead to the conclusion that the 540  
 541 Rayleigh oscillator shows sustained oscillations for param- 541  
 542 eters  $\gamma < 0$  and  $\delta > 0$ . 542

543 As shown in Fig. 4 the time series and trajectories of 543  
 544 the Rayleigh oscillator also exhibit relaxation behavior, but 544  
 545 in this case with a slow rise and fast drop. As for the 545  
 546 van-der-Pol, the phase space portrait is almost rectangu- 546  
 547 lar but the long and short axes are switched. Again the 547  
 548 power spectrum has peaks at the fundamental frequency 548  
 549 and contains odd higher harmonics. 549

550 Evidently, taken by themselves neither the van-der-Pol 550  
 551 nor Rayleigh oscillators are good models for human limb 551  
 552 movement for at least two reasons, even though they ful- 552  
 553 fill one requirement for a model: they have stable limit cy- 553  
 554 cles. First, human limb movements are almost sinusoidal 554





Movement Coordination, Figure 3

The van-der-Pol oscillator: time series (left), phase space trajectory (middle) and power spectrum (right)

555 and their trajectories have a circular or elliptical shape.  
 556 Second, it has also been found in experiments with hu-  
 557 man subjects performing rhythmic limb movements that  
 558 when the movement rate is increased the amplitude of the  
 559 movement decreases linearly with frequency [25]. It can be  
 560 shown that for the van-der-Pol oscillator the amplitude is  
 561 independent of frequency and for the Rayleigh it decreases  
 562 proportional to  $\omega^{-2}$ , both in disagreement with the exper-  
 563 imental findings.

564 It turns out that a combination of the van-der-Pol  
 565 and Rayleigh oscillator, termed the **hybrid oscillator** of the  
 566 form (13) fulfills all the above requirements if the param-  
 567 eters are chosen as  $\gamma < 0$  and  $\epsilon \approx \delta > 0$ .

568 As shown in Fig. 5 the time series for the hybrid oscilla-  
 569 tor is almost sinusoidal and the trajectory is elliptical. The  
 570 power spectrum has a single peak at the fundamental fre-  
 571 quency. Moreover, the relation between the amplitude and  
 572 frequency is a linear decrease in amplitude when the rate is  
 573 increased as shown schematically in Fig. 6. Taken together,  
 574 the hybrid oscillator is a good approximation for the tra-  
 575 jectories observed experimentally in human limb move-  
 576 ments.

### 577 The Coupling

578 As pointed out already, in a second step one has to find  
 579 a coupling function between two hybrid oscillators that  
 580 leads to the correct dynamics for the relative phase (2).  
 581 The most common realization of a coupling between  
 582 two oscillators is a spring between two pendulums, lead-  
 583 ing to a force proportional to the difference in locations  
 584  $f_{12} = k[x_1(t) - x_2(t)]$ . It can easily be shown, that such  
 585 a coupling does not lead to the required dynamics on the  
 586 relative phase level. In fact, several coupling terms  
 587 have been suggested that do the trick, but none of them  
 588 is very intuitive. The arguably easiest form, which is one  
 589 of the possible couplings presented in the original HKB  
 590 model [19], is given by

$$591 \quad f_{12} = (\dot{x}_1 - \dot{x}_2)\{\alpha + \beta(x_1 - x_2)^2\}. \quad (15)$$

592 Combined with two of the hybrid oscillators, the dynamical  
 593 system that describes the transition from anti-phase to  
 594 in-phase in bimanual finger movements takes the form

$$\begin{aligned} \ddot{x}_1 + \dot{x}_1(\gamma + \epsilon x_1^2 + \delta \dot{x}_1^2) + \omega^2 x_1 &= (\dot{x}_1 - \dot{x}_2)\{\alpha + \beta(x_1 - x_2)^2\} \\ \ddot{x}_2 + \dot{x}_2(\gamma + \epsilon x_2^2 + \delta \dot{x}_2^2) + \omega^2 x_2 &= (\dot{x}_2 - \dot{x}_1)\{\alpha + \beta(x_2 - x_1)^2\}. \end{aligned} \quad (16)$$

595 A numerical simulation of (16) is shown in Fig. 7. In  
 596 the top row the amplitudes  $x_1$  and  $x_2$  are plotted as a func-  
 597 tion of time. The movement starts out in anti-phase at  
 598  $\omega = 1.4$  and the frequency is continuously increased to  
 599 a final value of  $\omega = 1.8$ . At a **critical rate**  $\omega_c$  the anti-  
 600 phase pattern becomes unstable and a transition to in-  
 601 phase takes place. At the bottom a **point** estimate of the  
 602 relative phase  $\phi(t)$  is shown calculated as

$$603 \quad \phi(t) = \varphi_1(t) - \varphi_2(t) = \arctan \frac{\dot{x}_1}{x_1} - \arctan \frac{\dot{x}_2}{x_2}. \quad (17)$$

604 The relative phase changes from a value of  $\pi$  during the  
 605 anti-phase movement to  $\phi = 0$  when the in-phase pattern  
 606 has been established.

607 To derive the phase relation (2) from (16) is a little  
 608 lengthy but straightforward by using the ansatz (hypothesis)  
 609

$$610 \quad x_k(t) = A_k(t)e^{i\omega t} + A_k^*(t)e^{-i\omega t} \quad (18)$$

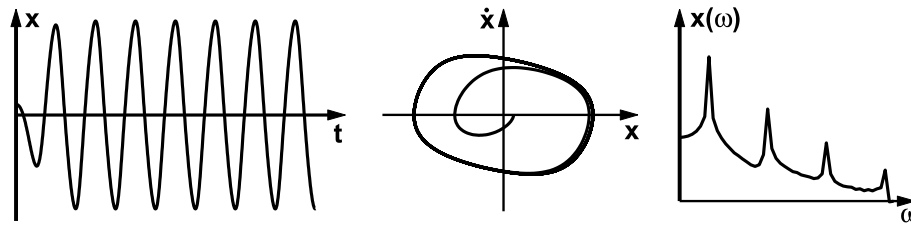
611 then calculating the derivatives and inserting them  
 612 into (16). ~~Then the~~ slowly varying amplitude approxima-  
 613 tion ( $\dot{A}(t) \ll \omega$ ) and rotating wave approximation (neg-  
 614 lect all frequencies  $> \omega$ ) are applied. Finally, introducing  
 615 the relative phase  $\phi = \varphi_1 - \varphi_2$  after writing  $A_k(t)$  in the  
 616 form

$$617 \quad A_k(t) = r e^{i\varphi_k(t)} \quad (19)$$

618 leads to a relation for the relative phase  $\phi$  of the form (2)  
 619 from which the parameters  $a$  and  $b$  can be readily found

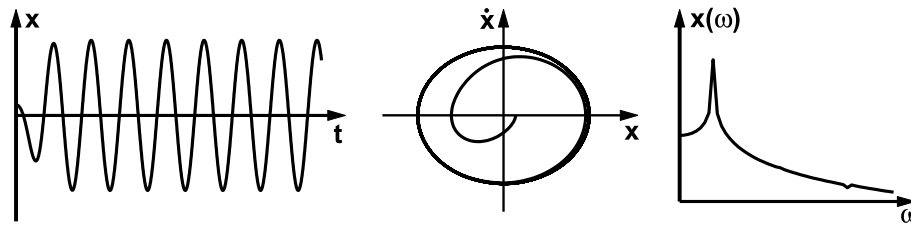






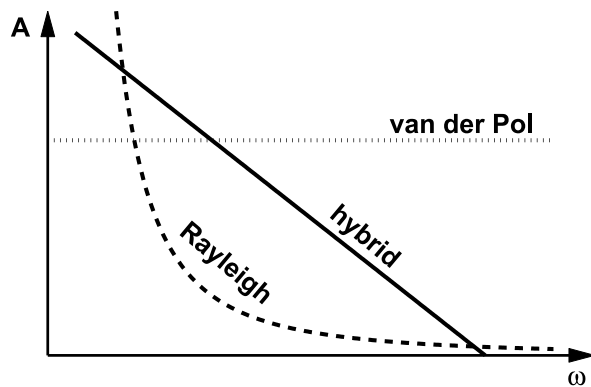
Movement Coordination, Figure 4

The Rayleigh oscillator: time series (left), phase space trajectory (middle) and power spectrum (right)



Movement Coordination, Figure 5

The hybrid oscillator: time series (left), phase space trajectory (middle) and power spectrum (right)



Movement Coordination, Figure 6

Amplitude-frequency relation for the van-der-Pol (dotted), Rayleigh ( $\sim \omega^{-2}$ , dashed) and hybrid ( $\sim -\omega$ , solid) oscillator

dinating components are identical, like two index fingers. As a consequence, the coupled system (16) has a symmetry: it stays invariant if we replace  $x_1$  by  $x_2$  and  $x_2$  by  $x_1$ . For the coordination between two limbs that are not the same like an arm and a leg, this symmetry no longer exists – it is said to be broken. In terms of the model, the main difference between an arm and a leg is that they have different **eigenfrequencies**, so the oscillator frequencies  $\omega$  in (16) are no longer the same but become  $\omega_1$  and  $\omega_2$ . This does not necessarily mean that during the coordination the components oscillate at different frequencies; they are still coupled, and this coupling leads to a common frequency  $\Omega$ , at least as long as the eigenfrequency difference is not too big. But still, a whole variety of new phenomena originates from such a breaking of the symmetry between the components [5,22,23,29,37].

As mentioned in Subsect. “The Coupling” the dynamics for the relative phase can be derived from the level of coupled oscillators (16) for the case of the same eigenfrequencies. Performing the same calculations for two oscillators with frequencies  $\omega_1$  and  $\omega_2$  leads to an additional term in (2), which turns out to be a constant, commonly called  $\delta\omega$ . With this extension the equation for the relative phase reads

621 in terms of the parameters that describe the oscillators and  
622 their coupling in (16)

623  
624 
$$a = -\alpha - 2\beta r^2, \quad b = \frac{1}{2}\beta r^2$$
  
625 with 
$$r^2 = \frac{-\gamma + \alpha(1 - \cos \phi)}{\epsilon + 3\delta\omega^2 - 2\beta(1 - \cos \phi)^2}. \quad (20)$$
  
626

627 **Breaking and Restoring Symmetries**

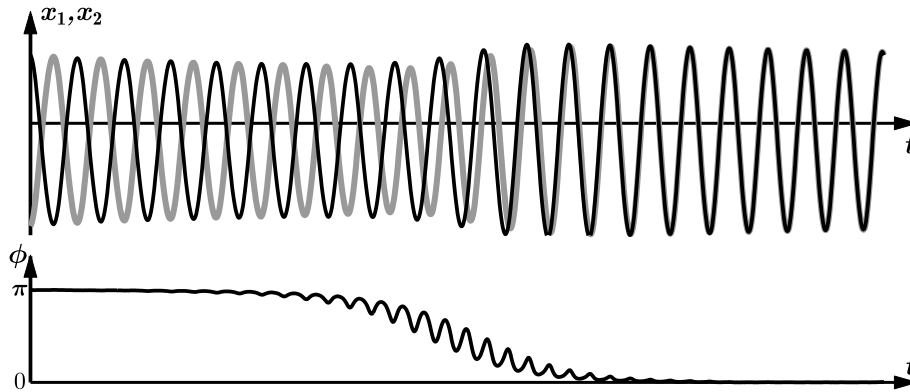
628 **Symmetry Breaking** Through the Components

629 For simplicity, the original HKB model assumes on both  
630 the oscillator and the relative phase level that the two coor-

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$$\dot{\phi} = \delta\omega - a \sin \phi - 2b \sin 2\phi$$

with 
$$\delta\omega = \frac{\omega_1^2 - \omega_2^2}{\Omega} \approx \omega_1 - \omega_2. \quad (21)$$



**Movement Coordination, Figure 7**

Simulation of (16) where the frequency  $\omega$  is continuously increased from  $\omega = 1.4$  on the left to  $\omega = 1.8$  on the right. *Top*: time series of the amplitudes  $x_1$  and  $x_2$  undergoing a transition from anti-phase to in-phase when  $\omega$  exceeds a critical value. *Bottom*: **Point** estimate of the relative phase  $\phi$  changing from an initial value of  $\pi$  during anti-phase to 0 when the in-phase movement is established. Parameters:  $\gamma = -0.7$ ,  $\epsilon = \delta = 1$ ,  $\alpha = -0.2$ ,  $\beta = 0.2$ , and  $\omega = 1.4$  to 1.8

659 The exact form for the term  $\delta\omega$  turns out to be the dif- 684  
 660 ference of the squares of the eigenfrequencies divided by 685  
 661 the rate  $\Omega$  the oscillating frequency of the coupled system, 686  
 662 which simplifies to  $\omega_1 - \omega_2$  if the frequency difference is 687  
 663 small. As before (21) can be scaled, which eliminates one 688  
 664 of the parameters, and  $\dot{\phi}$  can be derived from a potential 689  
 665 function

$$\begin{aligned} \dot{\phi} &= \delta\omega - \sin \phi - 2k \sin 2\phi \\ &\equiv \frac{dV(\phi)}{d\phi} \text{ with } V(\phi) = -\delta\omega \phi - \cos \phi - k \cos 2\phi. \end{aligned} \quad (22)$$

667 Plots of the phase space and the potential landscape for 697  
 668 different values of  $k$  and  $\delta\omega$  are shown in Figs. 8 and 9, 698  
 669 respectively. From these figures it is obvious that the symme- 699  
 670 try breaking leads to a vertical shift of the curves in phase 700  
 671 space and a tilt in the potential functions, which has sev- 701  
 672 eral important consequences for the dynamics. First, for 702  
 673 a nonvanishing  $\delta\omega$  the stable fixed points for the relative 703  
 674 phase are no longer located at  $\phi = 0$  and  $\phi = \pm\pi$  but are 704  
 675 now shifted (see Fig. 8). The amount of this shift can be 705  
 676 calculated for small values of  $\delta\omega$  and new locations for the 706  
 677 stable fixed points are given by

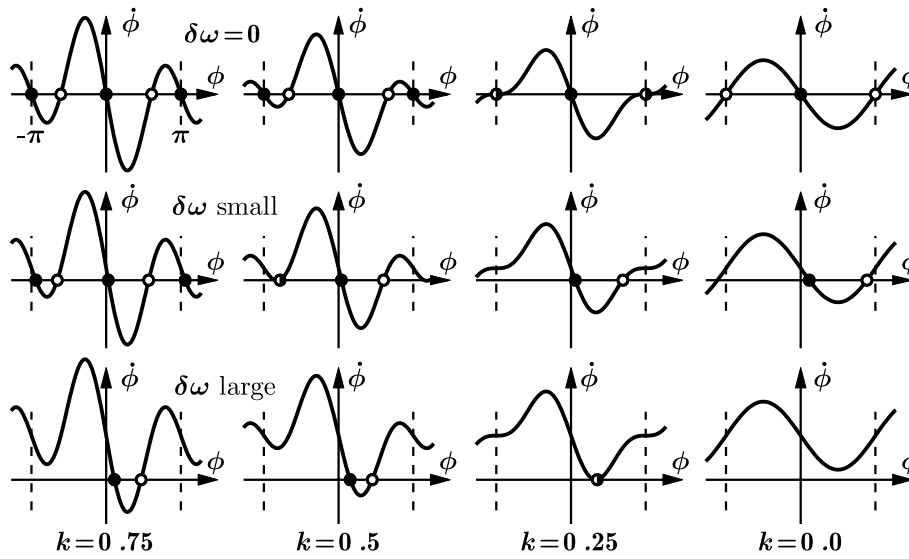
$$\phi^{(0)} = \frac{\delta\omega}{1 + 4k} \quad \text{and} \quad \phi^{(\pi)} = \pi - \frac{\delta\omega}{1 - 4k}. \quad (23)$$

679 Second, for large enough values of  $\delta\omega$  not only the fixed 711  
 680 point close to  $\phi = \pi$  becomes unstable but also the in- 712  
 681 phase pattern loses stability undergoing a saddle node bi- 713  
 682 furcation as can be seen in the bottom row in Fig. 8. Be- 714  
 683 yond this point there are no stable fixed points left and

the relative phase will not settle down at a fixed value any- 684  
 more but exhibit phase wrapping. However, this wrapping 685  
 does not occur with a constant angular velocity, which can 686  
 best be seen in the plot on the bottom right in Fig. 9. As 687  
 the change in relative phase  $\dot{\phi}$  is the negative derivative of 688  
 the potential function, it is given by the slope. This slope 689  
 is large and almost constant for negative values of  $\phi$ , but 690  
 for small positive values, where the in-phase fixed point 691  
 was formerly located, the slope becomes less steep indicat- 692  
 ing that  $\phi$  changes more slowly in this region before the 693  
 dynamics picks up speed again when approaching  $\pi$ . So 694  
 even as the fixed point has disappeared the dynamics still 695  
 shows reminiscence of its former existence. 696

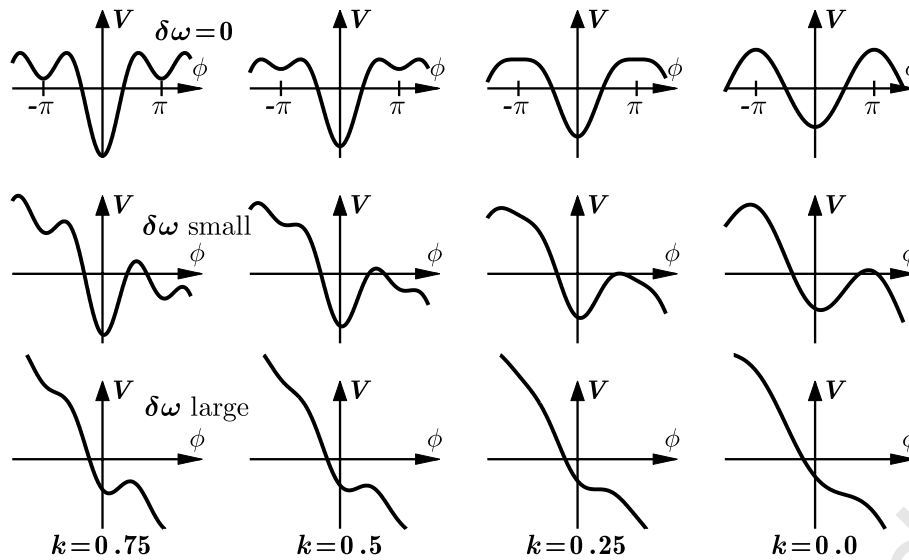
The dynamics of relative phase for the case of differ- 697  
 ent eigenfrequencies from a simulation of (22) is shown 698  
 in Fig. 10. Starting out at a slow movement rate on the 699  
 left, the system settles into the fixed point close to  $\phi = \pi$ . 700  
 When the movement rate is continuously increased, the 701  
 fixed point drifts upwards. At a first critical point a transi- 702  
 tion to in-phase takes place, followed by another drift, this 703  
 time for the fixed point representing the in-phase move- 704  
 ment. Finally, this state also loses stability and the relative 705  
 phase goes into wrapping. Reminiscence in the phase re- 706  
 gions of the former fixed point are still visible by a flatten- 707  
 ing of the slope around  $\phi \approx \pi$ . With a further increase of 708  
 the movement rate the function approaches a straight line. 709

The third consequence of this symmetry breaking is 710  
 best described using the potential function for small values 711  
 of  $\delta\omega$  compared to the symmetric case  $\delta\omega = 0$ . For the lat- 712  
 ter, when the system is initially in anti-phase  $\phi = \pi$  and  $k$  713  
 is decreased through its critical value a switch to in-phase 714  
 takes place as was shown in Fig. 1 (middle row). However, 715



**Movement Coordination, Figure 8**

Phase space plots for different values of the control parameters  $k$  and  $\delta\omega$ . With increasing asymmetry (top to bottom) the functions are shifted more and more upwards leading to an elimination of the fixed points near  $\phi = -\pi$  and  $\phi = 0$  via saddle node bifurcations at  $k = 0.5$  for small  $\delta\omega$  and  $k = 0.25$  for  $\delta\omega$  large, respectively



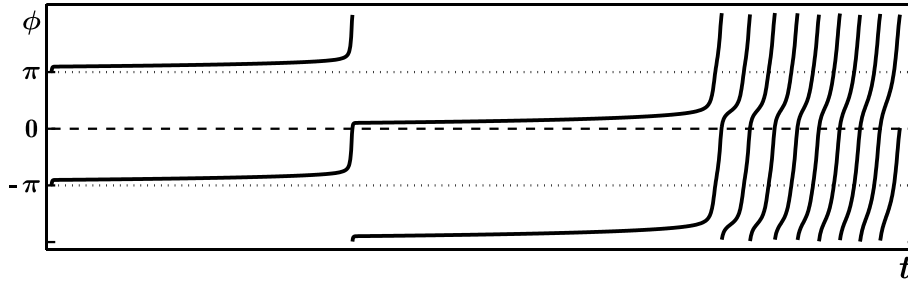
**Movement Coordination, Figure 9**

Potential landscape for different values of the control parameters  $k$  and  $\delta\omega$ . With increasing asymmetry (top to bottom) the functions get more and more tilted, destabilizing the system up to a point where there are no fixed points left on the bottom right. However, remnants of the fixed point can still be seen as changes in the curvature of the potential

716 the ball there does not necessarily have to roll to the left  
 717 towards  $\phi = 0$  but with the same probability could roll to  
 718 the right ending up in the minimum that exists at  $\phi = 2\pi$   
 719 and also represents an in-phase movement. Whereas the  
 720 eventual outcome is the same because due to the periodic-

ity  $\phi = 0$  and  $\phi = 2\pi$  are identical, the two paths can very  
 721 well be distinguished. The curve in Fig. 7 (bottom), showing  
 722 the point estimate of the relative phase during a transition,  
 723 goes from  $\phi = \pi$  down to  $\phi = 0$ , but could, in fact  
 724 with the same probability, go up towards  $\phi = 2\pi$ . In con-  
 725





**Movement Coordination, Figure 10**

Relative phase  $\phi$  as a function of time. Shown is a  $4\pi$  plot of a simulation of (22) for  $\delta\omega = 1.7$  where the control parameter  $k$  is continuously decreased from  $k = 2$  on the left to  $k = 0$  on the right. The system settles close to anti-phase and the fixed point drifts as  $k$  is decreased (corresponding to a faster period of oscillation). At a first critical value a transition to in-phase takes place followed by another fixed point drift. Finally, the in-phase fixed point disappears and the phase starts wrapping

726 trast, if the eigenfrequencies are different, also the points  
 727  $-\pi$  and  $\pi$ , and 0 and  $2\pi$  are no longer the same. If the  
 728 system is in anti-phase at  $\phi = \pi$  and  $k$  is decreased, it is  
 729 evident from the middle row in Fig. 9 that a switch will  
 730 not take place towards the left to  $\phi \approx 0$ , as the dynam-  
 731 ics would have to climb over a potential hill to do so. As  
 732 there are **random forces** acting on the dynamics a switch  
 733 to  $\phi \approx 0$  will still happen from time to time, but it is not  
 734 equally probable to a transition to  $\phi \approx 2\pi$ , and it becomes  
 735 even more unlikely with increasing  $\delta\omega$ .

736 These consequences, theoretically predicted to occur  
 737 when the symmetry between the oscillating components is  
 738 broken, can and have been tested, and have been found to  
 739 be in agreement with the experimental results [21,29].

#### 740 Asymmetry in the Mode of Coordination

741 Even though (16) is symmetric in the coordinating com-  
 742 ponents it can only describe a transition from anti-phase  
 743 to in-phase but not the other way around. Equation (16)  
 744 is highly asymmetric with respect to coordination mode.  
 745 This can be seen explicitly when we introduce variables  
 746 that directly reflect modes of coordination

$$747 \quad \psi_+ = x_1 + x_2 \quad \text{and} \quad \psi_- = x_1 - x_2. \quad (24)$$

748 For an in-phase movement we have  $x_1 = x_2$  and  $\psi_-$   
 749 vanishes, whereas for anti-phase  $x_1 = -x_2$  and therefore  
 750  $\psi_+ = 0$ . We can now derive the dynamics in the variables  
 751  $\psi_+$  and  $\psi_-$  by expressing the original displacements as

$$752 \quad x_1 = \frac{1}{2}(\psi_+ + \psi_-) \quad \text{and} \quad x_2 = \frac{1}{2}(\psi_+ - \psi_-) \quad (25)$$

and inserting them into (16), which leads to

$$\begin{aligned} \ddot{\psi}_+ + \epsilon\dot{\psi}_+ + \omega^2\psi_+ + \frac{\gamma}{12} \frac{d}{dt} (\psi_+^3 + 3\psi_+\psi_-^2) \\ + \frac{\delta}{4} (\dot{\psi}_+^3 + 3\dot{\psi}_+\dot{\psi}_-^2) = 0 \\ \ddot{\psi}_- + \epsilon\dot{\psi}_- + \omega^2\psi_- + \frac{\gamma}{12} \frac{d}{dt} (\psi_-^3 + 3\psi_-\psi_+^2) \\ + \frac{\delta}{4} (\dot{\psi}_-^3 + 3\dot{\psi}_-\dot{\psi}_+^2) \\ = 2\dot{\psi}_-(\alpha + \beta\psi_-^2). \end{aligned} \quad (26)$$

753 The asymmetry between in-phase and anti-phase is evi-  
 754 dent from (26), as the right-hand side of the first equation  
 755 vanishes and the equation is even independent of the cou-  
 756 pling parameters  $\alpha$  and  $\beta$ . This is the reason that the origi-  
 757 nal HKB model only shows transitions from anti-phase to  
 758 in-phase and not vice versa.

#### 759 Transitions to Anti-phase

760 In 2000 Carson and colleagues [6] published results from  
 761 an experiment in which subjects performed bimanual  
 762 **pronation-supination movements** paced by a metronome  
 763 of increasing rate (see also [2]). In this context an anti-  
 764 phase movement corresponds to the case where one arm  
 765 performs a pronation while the other arm is supinat-  
 766 ing. Correspondingly, pronation and supination with both  
 767 arms at the same time represents in-phase. In their exper-  
 768 iment Carson et al. used a manipulandum that allowed for  
 769 changing the axis of rotation individually for both arms as  
 770 shown in Fig. 11a. With increasing movement rate sponta-  
 771 neous transitions from anti-phase to in-phase, but not vice  
 772 versa, were found when the subjects performed prona-  
 773 tion-supination movements around the same axes for both  
 774 arms. In trials where one arm was rotating around the axis

above the hand and the other around the one below, anti-phase was found to be stable and the in-phase movement underwent a transition to anti-phase as shown for representative trials in Fig. 12.

It is evident that the HKB model in neither its original form (2) nor the mode formulation (26) is a valid model for these findings. However, Fuchs and Jirsa [11] showed that by starting from the mode description (26) it is ~~straight forward~~ to extend HKB such that, depending on an additional parameter  $\sigma$ , either the in-phase or the anti-phase mode is a stable movement pattern at high rates. The additional parameter corresponds to the relative locations of the axes of rotation in the Carson et al. experiment which can be defined in its easiest form as

$$\sigma = \frac{|l_1 - l_2|}{L} \quad (27)$$

where  $l_1$ ,  $l_2$  and  $L$  are as shown in Fig. 11b. In fact, any monotonic function  $f$  with  $f(0) = 0$  and  $f(1) = 1$  is compatible with theory and its actual shape has to be determined experimentally.

By looking at the mode Eqs. (26) it is clear ~~that~~ substitution  $\psi_+ \rightarrow \psi_-$  and  $\psi_- \rightarrow \psi_+$  to the left-hand side of the first equation leads to the left-hand side of the second equation and vice versa. For the terms on the right-hand side representing the coupling this is obviously not the case. Therefore, we now introduce a parameter  $\sigma$  and additional terms into (26) such that for  $\sigma = 0$  these equations remain unchanged, whereas for  $\sigma = 1$  we obtain (26) with all + and - subscripts reversed

$$\begin{aligned} \ddot{\psi}_+ + \epsilon \dot{\psi}_+ + \omega^2 \psi_+ + \frac{\gamma}{12} \frac{d}{dt} (\psi_+^3 + 3\psi_+ \psi_-^2) \\ + \frac{\delta}{4} (\dot{\psi}_+^3 + 3\dot{\psi}_+ \dot{\psi}_-^2) = 2\sigma \dot{\psi}_+ (\alpha + \beta \psi_+^2) \\ \ddot{\psi}_- + \epsilon \dot{\psi}_- + \omega^2 \psi_- + \frac{\gamma}{12} \frac{d}{dt} (\psi_-^3 + 3\psi_- \psi_+^2) \\ + \frac{\delta}{4} (\dot{\psi}_-^3 + 3\dot{\psi}_- \dot{\psi}_+^2) = 2(1 - \sigma) \dot{\psi}_- (\alpha + \beta \psi_-^2). \end{aligned} \quad (28)$$

From (28) it is straight forward to go back to the representation of the ~~finger~~ oscillators

$$\begin{aligned} \ddot{x}_1 + \dots = \frac{1}{2} (\ddot{\psi}_+ + \ddot{\psi}_-) + \dots \\ = \dot{\psi}_- (\alpha + \beta \psi_-^2) + \sigma \{ \dot{\psi}_+ (\alpha + \beta \psi_+^2) \\ - \dot{\psi}_- (\alpha + \beta \psi_-^2) \} \\ \ddot{x}_2 + \dots = \frac{1}{2} (\ddot{\psi}_+ - \ddot{\psi}_-) + \dots \\ = -\dot{\psi}_- (\alpha + \beta \psi_-^2) + \sigma \{ \dot{\psi}_+ (\alpha + \beta \psi_+^2) \\ + \dot{\psi}_- (\alpha + \beta \psi_-^2) \} \end{aligned} \quad (29)$$

where the left-hand side which represents the oscillators has been written only symbolically as all we are dealing with is the coupling on the right. Replacing the mode amplitudes  $\psi_+$  and  $\psi_-$  in (29) using (24) one finds the generalized coupling as a function of  $x_1$  and  $x_2$

$$\begin{aligned} \ddot{x}_1 + \dots = (\dot{x}_1 - \dot{x}_2) \{ \alpha + \beta (x_1 - x_2)^2 \} \\ + 2\sigma \{ \alpha \dot{x}_2 + \beta [\dot{x}_2 (x_1^2 + x_2^2) + 2\dot{x}_1 x_1 x_2] \} \\ \ddot{x}_2 + \dots = (\dot{x}_2 - \dot{x}_1) \{ \alpha + \beta (x_2 - x_1)^2 \} \\ + 2\sigma \{ \alpha \dot{x}_1 + \beta [\dot{x}_1 (x_1^2 + x_2^2) + 2\dot{x}_2 x_1 x_2] \}. \end{aligned} \quad (30)$$

Like the original oscillator Eq. (16), Eq. (30) is invariant under the exchange of  $x_1$  and  $x_2$  but in addition allows for transitions from in-phase to anti-phase coordination if the parameter  $\sigma$  is chosen appropriately ( $\sigma = 1$ , for instance), as shown in Fig. 14.

As the final step, an equation for the dynamics of relative phase can be obtained from (30) by performing the same steps as before, which leads to a modified form of the HKB equation (2)

$$\dot{\phi} = -(1 - 2\sigma)a \sin \phi - 2b \sin 2\phi \quad (31)$$

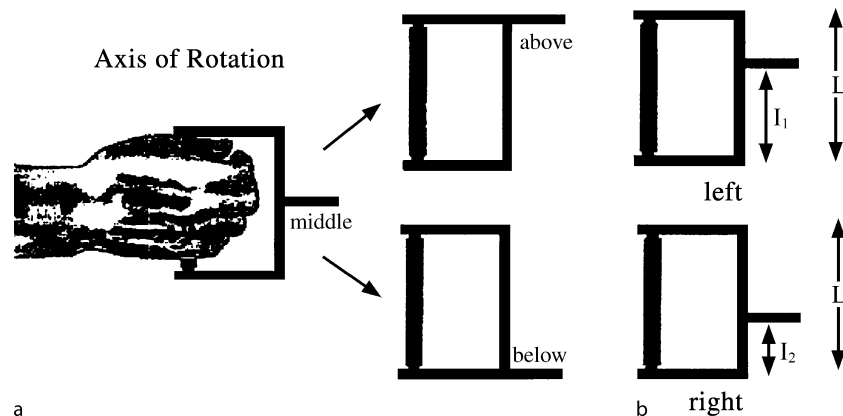
and the corresponding potential function

$$\begin{aligned} \dot{\phi} = - \frac{dV(\phi)}{d\phi} \\ \text{with } V(\phi) = -(1 - 2\sigma)a \cos \phi - b \cos 2\phi. \end{aligned} \quad (32)$$

Both equations can be scaled again leading to

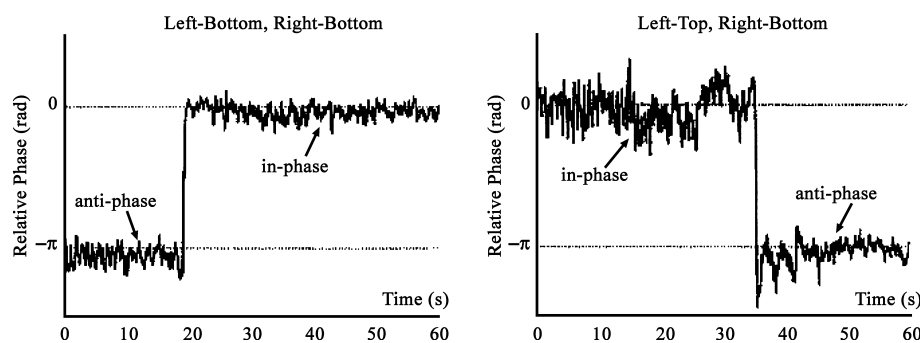
$$\begin{aligned} \dot{\phi} = -(1 - 2\sigma) \sin \phi - 2k \sin 2\phi \\ \equiv \frac{dV(\phi)}{d\phi} \quad \text{with} \\ V(\phi) = -(1 - 2\sigma) \cos \phi - k \cos 2\phi. \end{aligned} \quad (33)$$

The landscapes of the potential for different values of the control parameters  $k$  and  $\sigma$  are shown in Fig. 15. The left column exhibits the original HKB case which is obtained for  $\sigma = 0$ . The functions in the most right column, representing the situation for  $\sigma = 1$ , are identical in shape to the  $\sigma = 0$  case, simply shifted horizontally by a value of  $\pi$ . These two extreme cases are almost trivial and were the ones originally investigated in the Carson et al. experiment with the axes of rotation either on the same side or on opposite sides with respect to the hand. As the corresponding potential functions are shifted by  $\pi$  with respect to each other, one could assume that for an intermediate value of  $\sigma$  between 0 and 1 the functions are also shifted, just by a smaller amount. Such horizontal translations lead to fixed point drifts, as has been seen before



**Movement Coordination, Figure 11**

Manipulandum used by Carson and colleagues [6]. **a** The original apparatus that allowed for variation in axis of rotation above, below and in the middle of the hand. **b** The axis of rotation can be changed continuously, allowing us to introduce a parameter  $\sigma$  as a quantitative measure for the relative locations of the axes



**Movement Coordination, Figure 12**

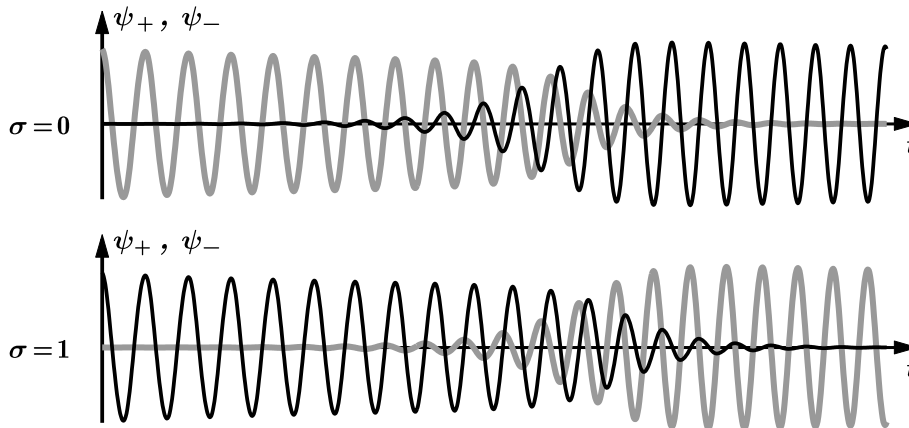
Relative phase over time for two representative trials from the Carson et al. experiment. *Left*: the axis of rotation is below the hand for both arms and a switch from anti-phase to in-phase occurs as the movement speeds up. *Right*: with one axis above and the other below the hand, the in-phase movement becomes unstable at higher rates leading to a transition to anti-phase

847 for oscillation components with different eigenfrequencies. The theory, however, predicts that this is not the case.  
 848  
 849 In fact, for  $\sigma = 0.5$  theory predicts that the two coordination modes in-phase and anti-phase are equally stable  
 850 for all movement rates. The deep minima for slow rates indicate high stability for both movement patterns and as  
 851 the rate increases both minima become more and more shallow, i. e. both movement patterns become less stable.  
 852  
 853 Eventually, for high rates at  $k = 0$  the potential is entirely flat, which means that there are no attractive states what-  
 854 soever. Pushed only by the stochastic forces in the system, the relative phase will now undergo a random walk. Note  
 855 that this is very different from the phase wrapping encountered before where the phase was constantly increasing  
 856 due to the lack of an attractive state. Here the relative phase will move back and forth in a purely random fash-  
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863 ion, known in the theory of stochastic systems as Brown-  
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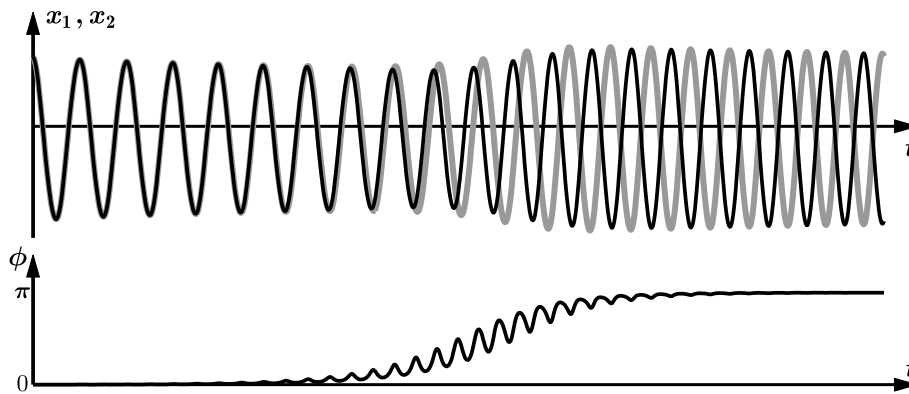
## Conclusions

869 The theoretical framework outlined above represents the  
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**Movement Coordination, Figure 13**

Simulation of (28) for  $\sigma = 0$  (top) and  $\sigma = 1$  (bottom) where the frequency  $\omega$  is continuously increased from  $\omega = 1.4$  on the left to  $\omega = 1.8$  on the right. Time series of the mode amplitudes  $\psi_+$  (black) and  $\psi_-$  (gray) undergoing transitions from anti-phase to in-phase (top) and from in-phase to anti-phase (bottom) when  $\omega$  exceeds a critical value. Parameters:  $\gamma = -0.7, \epsilon = \delta = 1, \alpha = -0.2, \beta = 0.2$ , and  $\omega = 1.4$  to  $1.8$



**Movement Coordination, Figure 14**

Simulation of (30) where the frequency  $\omega$  is continuously increased from  $\omega = 1.4$  on the left to  $\omega = 1.8$  on the right. Top: time series of the amplitudes  $x_1$  and  $x_2$  undergoing a transition from in-phase to anti-phase when  $\omega$  exceeds a critical value. Bottom: Point estimate of the relative phase  $\phi$  changing from an initial value of 0 during the in-phase to  $\pi$  when the anti-phase movement is established. Parameters:  $\gamma = -0.7, \epsilon = \delta = 1, \alpha = -0.2, \beta = 0.2, \sigma = 1$  and  $\omega = 1.4$  to  $1.8$

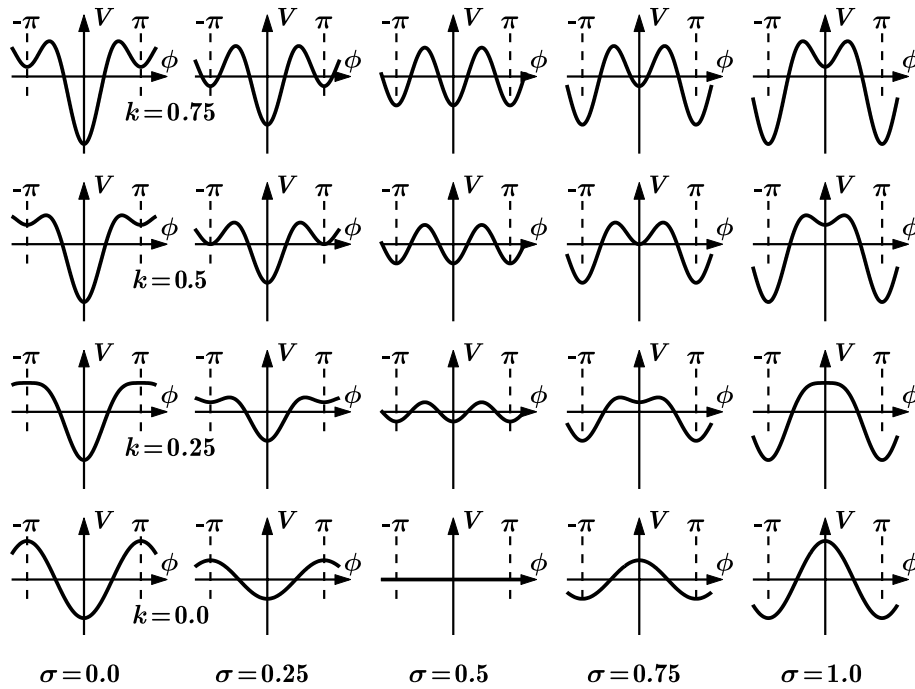
877 the mesoscopic level of the component oscillators and the  
 878 macroscopic level of relative phase allowed for quantita-  
 879 tive predictions and experimental tests with an accuracy  
 880 that is unprecedented in the life sciences, a field where  
 881 most models are qualitative and descriptive.

882 **Extensions of the HKB Model**

883 Beyond the phenomena described above, the HKB model  
 884 has been extended in various ways. Some of these exten-  
 885 sions (by no mean exhaustive) are listed below with a very  
 886 brief description; the interested reader is referred to the  
 887 literature for details.

- The quantitative description of the influence of noise on the dynamics given in Sect. “Stability: Perturbations and Fluctuations” can be done in a quantitative fashion by adding a stochastic term to (2) [40,43] or its generalizations (21) and (31) [11] and treating them as Langevin equations within the theory of stochastic systems (see e. g. [16] for stochastic systems). In this case the system is no longer described by a single time series for the relative phase but by a probability distribution function. How such distributions evolve in time is then given by the corresponding Fokker-Planck equation and allows for a quantitative description of the

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**Movement Coordination, Figure 15**  
Potential landscape for different values of the control parameters  $k$  and  $\sigma$

stochastic phenomena such as **enhancement of fluctuations** and **critical fluctuations**. An important quantity that can be derived in this context and is also related to the critical fluctuations is the mean-first-passage time, which is the time it takes (on average) to move over a hump in the potential function.

- When subjects flex a single finger between the beats of a metronome, i. e. syncopate with the stimulus, and the metronome rate is increased, they switch spontaneously to a coordination pattern where they flex their finger on the beat, i. e. synchronize with the stimulus. This so-called **syncopation-synchronization paradigm** introduced by Kelso and colleagues [32] has been frequently used in brain-imaging experiments.
- A periodic **patterning** <sup>CE3</sup> in the time series of the relative phase was found experimentally in the case of broken symmetry by Schmidt et al. [41] and successfully derived from the oscillator level of the HKB model [12,14].
- The metronome pacing can be explicitly included into (2) and its generalizations [24]. This so-called **parametric driving** allows us to explain effects in the movement trajectory known as anchoring, i. e. the variability of the movement is smaller around the

metronome beat compared to other regions in phase space [10]. With parametric driving the HKB model also makes correct predictions for the stability of **multi-frequency coordination**, where the metronome cycle is half of the movement cycle, i. e. there is a beat at the points of maximum flexion and maximum extension [1]. There ~~are~~ effects from more complicated polyrhythms that have been studied [38,39,47].

- The effect of symmetry breaking has been studied intensively in experiments where subjects were swinging pendulums with different eigenfrequencies [8,37,46].
- Transitions are also found in trajectory formation, for instance when subjects move their index finger such that they draw an “8” and this movement is sped up the pattern switches to a “0” [3,4,9].

**Future Directions**

One of the most exciting applications of movement coordination and its spontaneous transitions in particular is that they open a new window for probing the human brain, made possible by the rapid development of brain-imaging technologies that allow for the recording of brain activity in a noninvasive way. Electroencephalog-

**CE3** Is this correct or did you mean "patterning"?



946 raphy (EEG), magnetoencephalography (MEG) and func-  
 947 tional magnetic resonance tomography (fMRI) have been  
 948 used in coordination experiments since the 1990s to study  
 949 the changes in brain activations accompanying (or trig-  
 950 gering?) the switches in movement behavior [13,33,34].  
 951 Results from MEG experiments reveal a strong frequency  
 952 dependence of the dominating pattern with the contri-  
 953 bution of the auditory system being strongest at low  
 954 metronome/movement rates, whereas at high rates the  
 955 signals from sensorimotor cortex dominate [15,35]. The  
 956 crossover point is found at rates around 2 Hz, right where  
 957 the transitions typically take place.

958 In two other studies the rate dependence of the audi-  
 959 tory and sensorimotor system was investigated separately.  
 960 In an MEG experiment Carver et al. [7] found a resonance-  
 961 like enhancement of a brain response that occurs about  
 962 50 ms after a tone is delivered, again at a rate of about 2 Hz.  
 963 In the sensorimotor system a nonlinear effect of rate was  
 964 shown as well. Using a continuation paradigm, where sub-  
 965 jects moved an index finger paced by a metronome which  
 966 was turned off at a certain time while the subjects were  
 967 to continue moving at the same rate, Mayville et al. [36]  
 968 showed that a certain pattern of brain activation drops  
 969 out when the movement rate exceeds about 1.5 Hz. Even  
 970 though their contribution to behavioral transitions is far  
 971 from being completely understood, it is clear that such  
 972 nonlinear effects of rate exist in both the auditory and the  
 973 sensorimotor system in parameter regions where behav-  
 974 ioral transitions are observed.

975 Using fMRI brain areas have been identified that show  
 976 a dependence of their activation level as a function of rate  
 977 only, independent of coordination mode, whereas activa-  
 978 tion in other areas strongly depends on whether subjects  
 979 are syncopating or synchronizing regardless of how fast  
 980 they are moving [20].

981 Taken together, these applications of coordination dy-  
 982 namics to brain research have hardly scratched the sur-  
 983 face so far but the results are already very exciting as  
 984 they demonstrate that the experimental paradigms from  
 985 movement coordination may be used to prepare the brain  
 986 into a certain state where its responses can be studied.  
 987 With further improvement of the imaging technologies  
 988 and analysis procedures many more results can be ex-  
 989 pected to contribute significantly to our understanding of  
 990 how the human brain works.

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Uncorrected Proof  
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