

The logo graphic for 'Spektrum' consists of several overlapping, curved lines in blue, green, yellow, and red, suggesting movement or a spectrum of colors.

Spektrum

Bewegungswissenschaft



Jürgen Birklbauer

Optimal Variability for Effective Motor Learning

Band 9

MEYER
& MEYER
VERLAG

Spektrum Bewegungswissenschaft
Band 9

Optimal Variability for Effective Motor Learning

Dedicated to my father, Wilhelm Birklbauer,
who left us suddenly and far too early.

Spektrum Bewegungswissenschaft
Band 9

Jürgen Birklbauer

Optimal Variability for Effective Motor Learning

A Theoretical Review and Empirical Work
on Movement Variability

Meyer & Meyer Verlag

Herausgeber der Reihe Spektrum Bewegungswissenschaft:
Prof. Dr. Erich Müller, Universität Salzburg

Unterstützung durch die Stiftungs- und Förderungsgesellschaft
der Paris-London-Universität Salzburg

Bibliografische Information der Deutschen Nationalbibliothek

Die Deutsche Nationalbibliothek verzeichnet diese Publikation in der
Deutschen Nationalbibliografie; detaillierte bibliografische Daten sind im Internet
über <http://dnb.d-nb.de> abrufbar.

Alle Rechte, insbesondere das Recht der Vervielfältigung und Verbreitung sowie das
Recht der Übersetzung, vorbehalten. Kein Teil des Werkes darf in irgendeiner Form –
durch Fotokopie, Mikrofilm oder ein anderes Verfahren – ohne schriftliche Genehmigung
des Verlages reproduziert oder unter Verwendung elektronischer Systeme verarbeitet,
gespeichert, vervielfältigt oder verbreitet werden.

© 2019 by Meyer & Meyer Verlag, Aachen

Auckland, Beirut, Dubai, Hügendorf, Hongkong, Indianapolis, Kairo, Kapstadt,
Manila, Maidenhead, Neu-Delhi, Singapur, Sydney, Teheran, Wien



Member of the World
Sport Publishers' Association (WSPA)

Lektorat: Amnet Services

ISBN +) * %* &" %# \$+ #'

E-Mail: verlag@m-m-sports.com

www.wissenschaftundsport.de

www.dersportverlag.de

Table of Contents

From Theoretical Background to Practical Implications	11
1 Introduction	12
2 The Contextual Interference Effect	17
2.1 Potential moderating variables	19
2.1.1 Task (dis)similarity	20
2.1.2 Task complexity	21
2.1.3 Interaction of task similarity and task complexity	24
2.2 A couple of attempted explanations	28
2.3 Analyzing the neural basis by means of fMRI and TMS	32
3 The Differential Teaching and Learning Approach	38
3.1 Synergetics and coordination dynamics	39
3.1.1 Synergetic principles derived from inanimate nature	41
3.1.2 Non-linear dynamics of rhythmic uni- and bimanual coordination	44
3.1.2.1 Modeling coordination dynamics: the classic HKB model and its progression	47
3.1.2.2 Central neural correlates of relative phase dynamics	53
3.1.3 Phase transitions on short time scale: beyond standard finger coordination	61
3.1.3.1 Further control parameters and coordination constraints	61
3.1.3.2 From rhythmic interlimb through to discrete gross-motor coordination	63
3.1.3.3 Interpersonal coordination	66
3.1.3.4 On some further coordination domains of human nature	70
3.1.4 Phase transitions on medium time scale: motor and perceptual learning	73
3.1.4.1 Motor learning in the framework of coordination dynamics	74
3.1.4.2 The influence of initial coordination dynamics on learning and memory	75
3.1.4.3 Findings on gross-motor learning of continuous and discrete sport-related skills	81
3.1.4.4 Neural indices of learning-induced changes in coordination dynamics	83
3.1.4.5 Individual routes of learning-induced changes in perceptual dynamics	85
3.1.5 Phase transitions on long time scale: developmental psychology and psychotherapy	85
3.1.5.1 Anomalous variability as a harbinger of abrupt changes in child development ...	85
3.1.5.2 Detecting and using periods of anomalous variability in psychotherapy	90
3.2 Stochastic resonance	94
3.2.1 Generic theoretical models and characterization quantities	101

Table of Contents

3.2.2	Noise and its degree of (non-)determinism.....	105
3.2.2.1	Variability amplitude versus randomness using the example of postural control	108
3.2.2.2	The different colors of noise.....	109
3.2.2.3	1/f noise.....	116
3.2.3	Stochastic resonance and its origins in physics	125
3.2.4	The benefits of noise in biological functioning: simulations and experiments from ion channels to behavior	126
3.2.4.1	Optimal noise can improve neural processing	127
3.2.4.2	Optimal noise can improve sensory and perceptual processing.....	130
3.2.4.3	Optimal noise can improve behavioral processing in animals and humans.....	140
3.2.5	Stochastic resonance and the link to (differential) motor learning.....	148
3.3	Biological and computational neuroscience	152
3.3.1	Extracting rules out of experiences: the ability to generalize	152
3.3.2	Neural plasticity as the natural base for the generalization ability	156
3.3.2.1	The synaptic plasticity hypothesis.....	158
3.3.2.2	Synaptic changes: different mechanism on different time scales	162
3.3.2.3	Principles of plasticity or biological learning rules	169
3.3.3	Artificial neural networks: mathematical models of nature	174
3.3.3.1	Fundamental components and principles.....	175
3.3.3.2	Basis network architectures.....	177
3.3.3.3	Basic learning rules	180
3.3.3.4	Topographic mapping of common features.....	186
3.3.4	Associative memory, self-organization and generalization quality	205
3.3.4.1	Distributed memory storage.....	205
3.3.4.2	Self-organization: learning by examples.....	208
3.3.4.3	Validating generalization and some general factors of influence	211
3.3.5	Motor learning as the extraction of appropriate sensorimotor rules.....	213
3.3.5.1	The need for rule extraction even in closed conditions.....	213
3.3.5.2	Learning to utilize non-muscular forces.....	215
3.3.5.3	The whole may be different from the sum of its parts	218
3.3.5.4	The change of structuredness of execution variability during learning.....	219
3.3.6	Implicit generalization: an essential ability and ubiquitous phenomenon	224
3.3.6.1	Physical world comprehension.....	225
3.3.6.2	First language acquisition.....	227
3.3.6.3	Finite-state artificial grammars	232
3.3.6.4	Perceptual illusions.....	238
3.3.6.5	Superstition: extracting rules even if there are none	242
3.3.6.6	Logical reasoning even by relatively simple animals	243
3.3.6.7	Detecting abstract-rule-encoding neurons in monkeys.....	245

3.3.7 Interpolation is better than extrapolation	247
3.3.7.1 Concerning artificial neural networks.....	247
3.3.7.2 Concerning humans and animals	250
3.3.8 Meta-plasticity: changing the learning rate over time	259
3.3.8.1 The change of plasticity in natural learning.....	262
3.3.8.2 Meta-plasticity as a function of the learning process itself.....	263
3.3.9 A "perfect" memory: is it really desirable?.....	265
3.3.9.1 The problem of over- and underfitting in computational networks	266
3.3.9.2 When memorizing idiosyncratic details becomes patho-logical.....	271
3.3.9.3 Implications for (motor) learning	278
3.3.10 Random noise and its beneficial effects on neural network performance	279
3.3.10.1 Adding random noise to computational networks.....	279
3.3.10.2 From computational to biological networks.....	300
3.3.10.3 Simulated annealing.....	307
3.3.11 Simulating contextual interference by computational networks.....	348
3.3.11.1 Evaluating acquisition and retention.....	349
3.3.11.2 Evaluating generalization and relearning	351
3.3.11.3 Beyond the simple multi-layer perceptron.....	355
3.3.11.4 A brief résumé	359
4 Summary and Discussion	361
4.1 The seeming paradox of reducing noise by noise	363
4.2 The time-dependent structure of movement time series and the coupling between effectors.....	369
4.3 The predictive brain notion: forming a (causal) model of the world	377
4.4 The improvement of neural networks by random perturbations	397
4.5 The improvement of neural networks by structured variability	412
4.6 The contextual interference effect	430
4.7 The differential learning approach	447
Empirical Study	468
5 Statement of the Problem	469
6 Methods	475
6.1 Overall study design	475
6.2 Subjects	475
6.3 Intervention program.....	477

Table of Contents

6.4	Test design and data collection	492
6.5	Statistical analysis.....	493
7	Results	495
7.1	Target shooting.....	495
7.2	Slalom dribbling.....	497
7.3	Target shooting – slalom dribbling relationship	499
8	Discussion and Conclusion	501
	Bibliography.....	511
	Appendix A: questionnaire.....	598

Abstract

This thesis addresses different manifestations and practical implementations of movement variability in respect to their beneficial effects on movement coordination and learning. The focal point of this topic, which has been a long-standing, and still ongoing, issue of debate in academic research and among practitioners, is formed by the comparison between the contextual interference paradigm and the differential learning approach, representing two variable practice strategies found to improve motor learning performance under certain conditions. The theoretical backgrounds and empirical findings of each approach are thoroughly reviewed in the first part of this work. From contextual interference research, it is advised to frequently switch between different task variations during the acquisition phase in order to facilitate delayed retention and transfer. Established theoretical accounts are largely based on the cognitive-psychological perspective with the focus on the additional information-processing demands imposed by the changing context of practice. The literature review in this respect outlines evidence from actual neuroscientific findings and elaborates on major factors of influence, while arguing from the viewpoint of movement variability that the spatial variance and temporal structure of the task variations have to be tuned to the individual's inherent variability at the given task to advance learning. The differential training approach is conceived as a practical application of the fundamental ideas in synergetic and coordination dynamics, movement complexity analysis, stochastic resonance, and (artificial) neural network research. These basic concepts, which are introduced and discussed in the context of movement variability, led to a sustainable paradigm shift in motor science by highlighting variability as an essential functional entity of flexible and adaptive systems within different theoretical frameworks. Drawing on synergetic principles of self-organization, dynamical pattern theory identifies variability as a central feature for creating instabilities via which the movement system spontaneously shifts into qualitatively different organizational states on different time scales. The stochastic resonance framework elucidates the counterintuitive phenomenon of how random noisy perturbations can enhance the quality of information signals from positively impacting neuronal function to improving movement performance. Simulations by artificial neural networks, whose power rests upon their built-in generalization ability, provide valuable predictions for the selection of variable

and representative training stimuli, as well as for the addition of noise, in order to reasonably respond to unseen situations. These theoretical concepts, and their resultant practical training approaches, arrive at the notion of an optimal magnitude and structure of movement variability that should be encouraged during practice. The second part of this work presents a parallel-group study designed to contrast the effects of a high contextual interference and schema-based practice regime with two variants of differential training on the adoption of two indoor hockey skills in beginners. In relation to the contextual interference strategy that involved random practice of a discrete number of incrementally complex exercises, differential learners were confronted with an even larger amount of practice variability by increasing the differences between consecutive exercises that included erroneous movement executions and were performed only once in either a systematic or a random arrangement across multiple training sessions. Study results demonstrated positive acquisition and learning effects on target shooting and slalom dribbling for all three highly variable practice programs, with the improved criterion and transfer performance persisting over the 6-month retention interval except for random differential training. However, neither of the two differential training designs resulted in better acquisition, retention or transfer outcomes than the contextual interference approach. This supports the proposition that the amount of optimal practice variability is limited if the acquisition period is confined to several training sessions at the early stage of learning complex sport skills.

Part I

From Theoretical Background to Practical Implications

1 Introduction

Effective technique training and the resulting questions about optimized motor learning are of interest not only for competitive and recreational sports, but also for therapy and a vast number of occupational categories. This interest attracts particular attention in movement science; consequently, it is a great challenge of such research to develop a practicable learning strategy to achieve a certain skill at best.

At least since Schmidt's schema theory and the resulting development of the variability-of-practice hypothesis (postulated in 1975), variable practice has become well accepted learning strategy, even for closed skills.

N. A. Bernstein already mentioned in 1947, that the uncontrollable dynamics of the environment is in contrast to any possibility of a standardized motor formula being imprinted in the brain. According to Bernstein, one should take into account that forces producing a certain movement output are not predefined only by the muscles' innervation state and their length and velocity at a given time. Apart from those active muscle forces, passive external and internal dynamics such as position-dependent gravitational forces and mechanically reactive or motion-dependent forces (i.e. inertial, centrifugal and Coriolis forces), as well as passive forces arising from muscle deformation and other soft tissues are (inter)acting as well, resulting in an equivocal relationship between the innervational impulses and the movement outcome. Expressed another way, more than one motor signal can lead to the same movement trajectory and vice versa: identical motor signals can cause different movements under non-identical initial conditions and/or in the presence of variations in the external force field.

By modeling performance optimization, Hatze (1986) pointed out that it is impossible to determine, solely from motion observation, which actions and neural activity generated the observed motion, and emphasized that "exact repetitions of motions are not possible". In a couple of empirical studies, Schöllhorn and colleagues took a holistic approach for non-linear analysis of different complex movement patterns that convincingly indicated a low probability of executing two identical movements. Even in top athletes, time series and artificial neural network analyses of relatively short movement phases affirmed

the individuality of movement patterns over a period of up to 1 year, including pole vault (Jaitner & Schöllhorn 1997); contact phase in long jump (Jaitner et al. 2001); the final throwing phase of discus (Bauer & Schöllhorn 1997; Schöllhorn 1998) and javelin (Schöllhorn & Bauer 1998); a double step in running (Schöllhorn 1999a); free throw in basketball (Schmidt et al. 2009); as well as sprint (Simon & Schöllhorn 1997) and gait patterns during ground contact (Janssen et al. 2008; Janssen et al. 2011; Schöllhorn et al. 2002); finger and whole-body kinematics in flute playing (Albrecht et al. 2014); and tactical patterns in team sports (Jäger & Schöllhorn 2012).

Regarding altered initial conditions or reactive forces, the task requirements are permanently changing, even though the environment is kept constant. Such changes occur to a greater extent in more complex movements than in laboratory motor tasks because the relationship between central impulses and the movement outcome is “further removed from unequivocality” (Bernstein 1967, p. 21) in an exponential progression by each new degree of freedom of the kinematic chain. Against this background, it is not surprising that motor program concepts, and from there constant practice, are predominantly established in typical psychological test settings with simple motor tasks (cf. Wulf & Shea 2002; Birklbauer 2006). It is further obvious that even in closed skills, the number of executable solutions to a given motor task always far exceeds the small number of learned examples (motor redundancy). Hence, it is the objective and the challenge, not only in open skills, but also in more standardized motor tasks, to necessarily develop a task-specific interpolation ability to adequately and rapidly react to new situations in terms of changing external and internal forces acting on the body. The development of such, of course, neurally based rules is a central element in Schmidt’s schema theory, and consequently, in the variability-of-practice hypothesis, as well as in a more recent approach of so-called differential learning by Schöllhorn (1998, 2000), although both concepts approach from different research fields and differ in some key aspects, and hence lead to different consequences.

First of all, in contrast to the schema theory, in differential learning the nature of the rules that have to be acquired for a successful adaptation to changing constraints is not a priori determined, but emerges by itself only by interaction of the subsystems in a self-organized manner (cf. Frank et al. 2008). Furthermore, the schema theory does not explain the variability-of-practice effect in

tasks where the environment is kept constant. Neglecting persistently varying position-dependent and motion-dependent forces restrains the application of prior predefined invariants to a limited number of movements that are almost exclusively generated by muscular forces. On the contrary, when moving in complex and dynamic performance contexts, the variations of Schmidt's predefined invariants are unavoidable (cf. Schöllhorn et al. 2007c).

Schöllhorn's differential learning and teaching is based on the system dynamic approach; it intends to apply the principles of self-organization, introduced in the 1960s by H. Haken (1983) and transferred to motor science in the 1980s by J. A. S. Kelso (1995), into practice of motor learning and technique training. Quite similar to Bernstein, who concluded that practice is a particular type of repetition without repetition by means of repetitively solving the same problem in different manner, the central postulation of differential learning concerns the intention of "never repeating an exercise twice" (Trockel & Schöllhorn 2003), which is not possible anyway, as was previously stated. However, with an increase in execution variability, differential learning seeks to more extensively scan the hypothetical solution space of a given task, encouraging the learner to gain appropriate neuronally coded rules that enable a context-dependent optimized use of external and reactive forces, and therefore, reliable and successful solutions of complex skills. Consequently, the construct of differential learning is mainly characterized by Schöllhorn et al. (2009b) as randomly adding variable elements to target movements.

While the variability-of-practice hypothesis corresponds to the comparison between variable and constant practice and offers no provision of how the order-of-practice trials should be conducted, the context interference effect refers to the effectiveness of different variable practice schedules. It originates in observations that practicing different exercises or tasks in a randomized order, compared to a blocked practice schedule, impedes acquisition, but favors retention and transfer performance. Different amounts of interference emerging from performing variations within the context of practice are seen as a continuum between two extremes: high contextual interference, wherein the sequence of exercises would be randomly assessed, and low contextual interference resulting from the practice of each task variation within its own block, or unit, of time (cf. Magill 2007). Various forms of serial practice (e.g. a serial order of task or block variations) organize variable practice between both ex-

tremes. Whereas the contextual interference effect is related to the order of exercises, their selection and other parameters act as moderator variables. The effect of different contextual interference on learning and memory roots in experimental cognitive psychology. It was first described by Battig (1966, 1972) in verbal learning, and brought forward to motor learning by Shea and Morgan (1979) in a serial reaction and movement time task.

In terms of differential learning, contextual interference is considered as a noise generating practice schedule in which randomized order, defined as high contextual interference, induces a higher level of noise than blocked order does. Whereas traditional models view noise as inherent changes of a given target movement, in differential learning noise also includes the instructed movement variations, traditionally referred to as variability (Schöllhorn et al. 2006a). In two case studies, Gebkenjans et al. (2007) and Janssen et al. (2010) demonstrated that executions of first and second tennis services in a serial order led to higher variance of each technique than a blocked arrangement; therefore, they cover a greater area of potential solutions. In a bifurcation model of differential learning on a dynamic system perspective by Frank et al. (2008), or in an evolving landscape approach including simulated annealing processes by Schöllhorn et al. (2009b), the amount of noise must exceed a particular threshold to enable further learning progress. Therein, training noise represents the variety of between-exercise difference.

The amount of contextual interference, as well as noisiness, not only depends on exercise schedule, but also depends strongly on the types of exercise. In most studies on the contextual interference effect, exercises are selected with regard to Schmidt's schema theory intending to develop and to automatize a generalized motor program, or to differentiate between different programs. A contrasting juxtaposition of task variations between different motor programs (program variable practice) and variations within the same motor program (parameter variable practice) has been a key issue in past research since Magill and Hall (1990) proposed this hypothesis in relation to task difficulty.

Against the contextual interference approach, where exercises are picked due to program parameters, differential learning does not focus only on the variation of movement parameters or movement invariants; nor do exercises belong to a particular movement class. From a system dynamics' point-of-view, predefined movement classes or schemata do not exist. In contrast, in differ-

ential learning, subjects experience as many different invariant and variable parameters as possible, which leads to the knowledge of a larger pool of potential solutions. Therefore, Schmidt's variable practice is only a small subset of differential training, which, as defined by Schöllhorn (2000) and Schöllhorn et al. (2007c), involves all forms of variable and constant learning approaches. Schöllhorn et al. (2009b) consider traditional learning approaches, including constant practice and methodical rows of exercises, as well as different schedules of variable practice as different levels of stochastic perturbations, whereby the highest level is achieved with the differential learning strategy.

As mentioned above, the contextual interference approach concerns the organization of a certain selection of exercises, but is essentially influenced by the character of the exercises themselves. The contextual interference hypothesis does not imply a predefined number of variations; rather, it compares different practice schedules that contain the same exercises and the same total number of executions per variation. Previous studies used a limited number of three to four variations. If their number is increased and the character of variations is not taken into consideration, contextual interference approach advances toward differential learning.

In contrast to the observed contextual interference effect where randomized practice showed worse performance in the acquisition phase, the differential learning approach postulates not only superior retention and transfer, but also acquisition performance. This may occur if the learning environment is noisy enough to extensively scan the hypothetical solution space of the task (cf. Schöllhorn et al. 2006a; Frank et al. 2008; Schöllhorn et al. 2009b). As indicated by Gebkenjans et al. (2007) in tennis and Beckmann et al. (2010) in hockey, contextual interference or noise must be optimized, not maximized, for maximal learning success; that is, an inverted U-shaped relationship between the amount of noise and learning performance. Contextual interference supports that notion by showing worse results when interference exceeds a certain level, depending on the task to be learned and the performance level (see Chap. 2.1). This raises the question of whether and how to structure the training progress.

2 The Contextual Interference Effect

After the early findings of Battig (1972) and Shea and Morgan (1979), a considerable number of studies on the contextual interference effect were conducted in different conditions leading to several extensive reviews and meta-analyses. However, at issue results caused by a multitude of moderator variables pose more questions than answers.

Contextual interference effect meta-analyses were conducted by Wiemeyer (1998) with 112 effect sizes out of 63 studies; by Brady (2004) with 139 effect sizes out of 61 studies; by Mazzardo (2004) with 115 effect sizes out of 51 studies; and by Lin (2006) with 336 estimates of effect sizes out of 122 studies. All studies included in those analyses were published from 1979 to 2005, but they differed considerably across meta-analyses. The fewest identical studies were found between Wiemeyer and Mazzardo with 36%, whereas the Mazzardo had 64% in common with Brady representing the highest concordance (cf. Fig. 1). Only 18% of the studies were analyzed in all four meta-analyses. The results of those analyses should be compared with caution despite the fact that the same effect size was used calculating Cohen's d corrected for bias and sample size by Hedges and Olkin (1985). Mazzardo set effect sizes being not significant as zero yielding in a possible underestimation of the contextual interference effect. Brady put scores for retention and transfer tests in a single analysis, and thus violated the independence assumption of standard meta-analysis.

The overall contextual interference effect is supported and warranted by significant overall mean effect sizes over acquisition, retention and transfer. In accordance with the contextual interference hypothesis, the blocked group outperformed the random group in acquisition with small to medium effects stated by Mazzardo ($-.31$) and Lin ($-.42$), whereas Wiemeyer found a large mean effect ($-.84$). For retention and transfer, the mean treatment effect was similar and of small to moderate size in Brady's ($.40/.31$), Mazzardo's ($.31/.23$) and Lin's ($.31/.28$) analyses, but once again larger in Wiemeyer's study ($.56/.43$), which may be explained by the least study concordance with the other three meta-analyses.

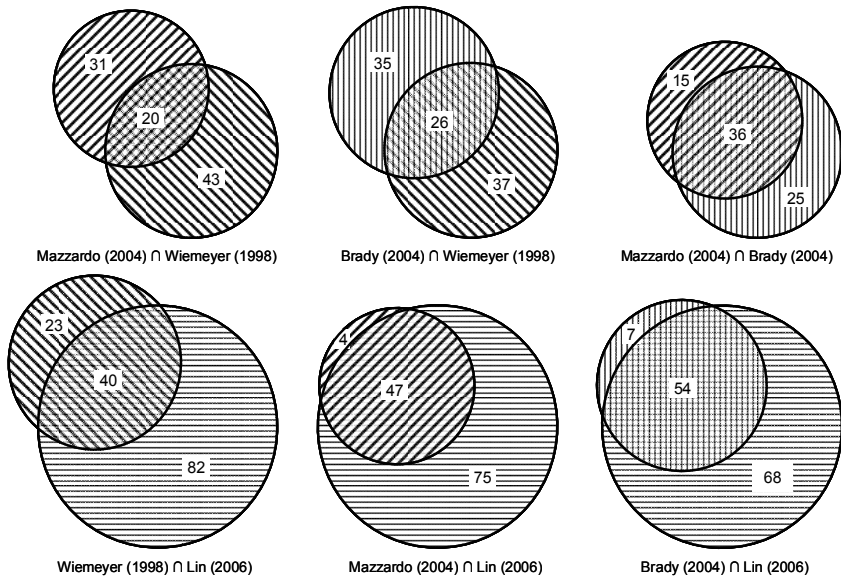


Fig. 1: Intersections of the analyzed literature in the contextual-interference meta-analyses by Brady (2004), Lin (2006), Mazzardo (2004) and Wiemeyer (1998)

Tests for homogeneity done by Wiemeyer, Brady and Lin to assess whether all the effect sizes were similar revealed that the overall effects were inhomogeneous in acquisition, retention and transfer, indicating that some other factors (i.e. moderator variables) influence the contextual interference effect. To estimate the publication bias, Wiemeyer and Brady calculated the fail-safe N in order to answer the so-called file drawer problem that represents the number of unpublished studies with null effect that would be necessary to reduce the cumulated effect size to a non-significant level. Brady found a fail-safe N of 204 for the overall effect including retention and transfer, so it is unlikely that there are that many studies sitting in file drawers. This is in accordance with Wiemeyer's results in acquisition and retention; however, for transfer, the validity of the effect sizes is not supported. Additionally, Brady calculated the overall mean power of the studies reviewed based on an estimated effect size of .40. An overall beta error of .57 indicates a lack of adequate sample size, especially in those studies where the effect size is small.

2.1 Potential moderating variables

Due to the inhomogeneous results of contextual interference studies, multiple moderator variables were theoretically debated and their influence was calculated if the number of studies was sufficient. Such variables are ecological and internal validity; amount of practice and contextual interference; type of skill, test and task; skill level; age; gender; knowledge of result; personality; and theoretical explanations.

The only moderator variable that was analyzed in all four cited meta-analyses belongs to the nature of research or ecological validity. Whereas in acquisition, significant larger contextual interference effects were consistently revealed in laboratory oriented research than applied, the meta-analytic studies disagreed in retention. Wiemeyer and Brady found again bigger advantages for random practice for settings lacking real-world features (2.4 to 3 times as many mean effects), while Mazzardo and Lin demonstrated similar magnitude of effect sizes. A possible explanation for this disagreement could be provided by the different inclusion of applied studies. Contrary to Mazzardo and Lin, in Wiemeyer's and Brady's analyses applied studies contained only real sport settings and tasks. As typical sport skills are more often of complex nature with a higher degree of freedom, random practice more likely leads to a mental overload through movement variability.

Furthermore, Brady established an interaction of age and nature of research; that is, young learners showed relatively small effect sizes in applied sport settings; however, when the comparison is limited to adults, the effect size differences between laboratory and applied studies are of less magnitude. Besides Brady's revealed age difference in contextual interference effect, Lin could confirm larger effects for adults even though in acquisition, but neither in retention nor in transfer. The observation that the movement variability induced through random practice schedule overwhelms the learner's capability as seen in age could be further expanded to novices and female. As Lin pointed out, male or experienced had two to three times larger effects sizes in retention being moderate to large.

Brady detected in a comparison between different amounts of contextual interference that high amounts were more effective than mixed, but not when sport skills were taught. Mean effect sizes differed also across different types

of tests and different amounts of practice. Against precision tasks, Wiemeyer calculated about two times larger effects for tasks with focus on movement speed in retention and three times larger effects in transfer. Although Mazzardo and Lin classified the amount of practice equally, their results diverged favoring, on the one hand, medium amount studies with 51 to 90 trials; and on the other hand, studies with larger amounts.

Neither during acquisition nor retention or transfer did the presence or absence of augmented feedback significantly influence effect sizes, as Mazzardo unveiled; however, different types of knowledge of result were not distinguished. The analysis of the internal validity demonstrated higher effect sizes in studies where participants, tasks and the methodological procedures were more tightly controlled, which could have been expected.

2.1.1 Task (dis)similarity

Based on the extended review of different types of tasks, Magill and Hall (1990) recognized that the contextual interference effect is not a global effect and may be manipulated by the type of task variations to be practiced. Their “between- vs. within-motor program hypothesis” is related to the diverse similarity or dissimilarity of task variations and the thereof derived task difficulty, which generates different amounts of contextual interference. When the variations to be practiced in random order are quite different (i.e. requiring different generalized motor programs) a higher level of contextual interference is created leading to enhanced retention and transfer performances. However, if the task variations are similar involving parameter modifications, which are within the same motor program, the contextual interference effect due to reduced task difficulty will not be found. Based on the assumption that varying between different motor programs requires the reconstruction of the program inclusive parameter adjustments each time, learners engage in more effortful processing than when the task variations are similar.

Wiemeyer and Mazzardo confirmed in their meta-analytic studies for both parameter variable and program variable practice contextual interference effects. While parameter alterations during practice yielded in small results, varying between different movement patterns produced more than two times larger effects in retention and transfer, although negative effect sizes did not differ in acquisition phase. In an early laboratory experiment, Wood and Ging (1991)

directly compared different levels of similarity of the task variations to be learned. Results of the retention and novel transfer tests supported contextual interference effects for low, but not high, similarity tasks. In place of defining task similarity as a function of the spatial characteristics (i.e. size versus shape) of the movement patterns, Boutin and Blandin (2010a) more recently compared parameter variable practice of more or less similar absolute movement times in a three-segment timing task. While no blocked-random difference was found for the similar parameter condition, varying more dissimilar target times produced higher intertrial variabilities during acquisition with the highest by random practice, and again, a typical contextual interference effect. In both studies, however, task variations were restricted to simple skills with few degrees of freedom, or even to the same motor program which thus may induce lower movement variability by itself.

In contextual interference literature, parameter learning is sometimes equated with parameter variable practice and program learning with program variable practice, respectively. In order to avoid confusion, this should be separated. Whereas the parameter or program variable practice refers to the properties of the variation, program or parameter learning refers to what is learned through practice, that is, the construction of particular motor programs or the improvement of parameter modification within motor programs.

Magill and Hall's view concerning the superiority of program variable practice predicts that both program learning and parameter learning would be enhanced in contrast to parameter variable practice. When programs are reconstructed, parameters added to them have to be modified as well. Opposing this prediction, contextual interference effects were mostly detected in parameter learning, but not in program learning, regardless of whether skill variations are controlled by the same or different programs (cf. Mazzardo 2004). However, those studies, which drew the comparison between both kinds of learning practicing within or between motor programs, used serial practice schedules as high contextual interference and very simple laboratory tasks.

2.1.2 Task complexity

Besides the subjects' skill levels and ages, the difficulty or amount of interference created during practice depends on the complexity of a given task. This

probably caused, as Hebert et al. (1996) stated, different results between laboratory and applied research settings.

The topic was taken up by Wulf and Shea (2002) in their extended review about the different properties of simple and complex skill learning. As opposed to laboratory experiments of the contextual interference effect that involve typically multi-segment tasks, simple aiming and anticipation-timing tasks or movement patterning and tracking tasks, complex skills feature several degrees of freedom, cannot be mastered in a single session and tend to be ecologically valid as categorized by Wulf and Shea (2002). According to their view, practicing more complex movement patterns calls for higher attention, motor control and memory demands, which make those tasks themselves more difficult, especially when learners are relatively inexperienced. More demanding practice schedules like random practice may, therefore, overload learners' capacities and thus diminish the advantages of high contextual interference schedules.

Albaret and Thon (1998) corroborated the hypothesis that the complexity of the task to be learned modulates the contextual interference effect. Comparing random and blocked practice in different levels of complexity of a laboratory drawing task, retention and transfer tests revealed a clear advantageous effect for random practice, but only in the simplest condition. When the task complexity was increased, the random practice benefits were reduced and in the most complex condition almost reversed. Similar results were reported more recently by Boutin and Blandin (2010b) for a timing task whose target times had to be performed either in one single or three different movement directions with the latter being more complex due to its higher degrees of freedom. While practicing the simple task variants yielded a typical contextual interference effect, no blocked-random difference was found for the more complex movement pattern regardless of the amount of practice. Furthermore, advantages of random relative to blocked practice are all the more lost, when the complexity and difficulty of the task is increased by producing both a goal movement outcome and a specific relative force or timing pattern (Wulf & Shea 2002).

From a cognitive-psychological perspective, Wulf and Shea (2002) interpreted those findings to the effect that with an excessive degree of complexity in movement task and practice schedule, the development of memory represen-

tations or motor programs would be degraded. This is because, on the one hand, short-term memory may be overloaded, limiting motor processing or elaboration or on the other hand, make a full reconstruction from trial to trial difficult. In the “challenge-point” framework postulated by Guadagnoli and Lee (2004) from an information-theoretical point of view, task complexity relates to the constant, nominal task difficulty while the functional difficulty of a given task additionally depends on the skill level of the performer and the conditions under which the task is being practiced. For optimal learning, practice conditions, such as the trial order, need to be adjusted to one’s information-processing capabilities, which in turn is a function of the skill level, and the nominal task difficulty such that an optimal amount of interpretable information is available (i.e. the optimal challenge point). For instance, a complex task or a random trial order will increase the functional task difficulty, and thus, will provide for more information generated in the performance of the task because more uncertainty can be reduced. Still, beyond an individual’s optimal challenge point, further increase of potential information would be increasingly noninterpretable as it overflows the information-processing capacity of the learner resulting in less learning benefit. As such, random practice of a complex task may offer an appropriate functional difficulty for an expert performer, whereas it would presumably overshoot the amount of information efficiently processed by a beginning performer. Practicing a simple task in a constant or blocked manner without changing environmental conditions, on the other hand, might be functionally too easy for novices and even more so for advanced performers; again, precluding the individual from his/her optimum challenge point for learning. But this time because, rather than too much, too little potential information is available as there is high certainty about the potential success of performance. From a dynamical system point of view (see Chap. 3.1), the combination of inherent variability and introduced variability – the first caused among others by the task complexity and the second by the practice schedule – might exceed an optimal level of movement variability or noise. Such an excessive amount of noise would then rather impede than enhance the development of the task-specific interpolation ability necessary to successfully adapt to changing constraints.

2.1.3 Interaction of task similarity and task complexity

Introduced variability is not only determined by the practice schedule (i.e. constant, blocked, serial or random practice), but also by the similarity or dissimilarity of the task variations. Given a complex task setting, variations to be practiced with small similarity and in random order would predict a tremendous amount of movement variability. That might exceed the optimal level of noise; therefore, it impedes learning, whereas the same amount of introduced variability in laboratory tasks might be optimal noise, and thus, enhance learning.

According to already mentioned Magill-and-Hall-hypothesis (1990), in laboratory-based research high contextual interference is more effective than low when tasks using different motor responses are performed. Contrarily, in research using complex sport skills the contextual interference effect could be demonstrated, in particular, when variations were within the same motor program; hence, it is relatively similar. This fact is supported by a meta-analysis by Gelber (2005) including 27 applied studies published between 1986 and 2004, where it was differentiated between the type of exercises (i.e. within the same or between different generalized motor programs).

Fifty-seven mean effect sizes weighted by sample size were calculated for acquisition, retention and transfer. Taking both types of tasks together, a similar, but slightly lower mean effect size of .14 was discovered in retention than Brady (2004) found for field-based research. Mean effects in acquisition (.02), as well as transfer (.10) were below .20 – representing small and trivial differences as defined by Cohen (1988), where results in acquisition were quite similar to Wiemeyer (1998), Mazzardo (2004) and Lin (2006). However, by differentiating between task types and taking only complex sport settings into account as a higher inherent variability is assumed, the contextual interference effects were apparent only in parameter variable practice (see Fig. 2). In comparison to the ten studies varying between different skills, the 13 parameter altering studies showed notably higher contextual interference effects for acquisition (–.17), retention (.38) and transfer (.19), whereas program variable practice fails to achieve mean effects for acquisition (–.03), for retention (.04) or for transfer (.01).

The assumption that varying different motor responses combined with high task complexity leads to a noise overload (i.e. exceeding the optimal level of

movement variability) is brought forward by a self-performed research review. Twenty-six applied studies related to complex sport skills, published between 1984 and 2007, were analyzed in the style of a traditional voting method. Fourteen of those 26 studies involved similar variations within one skill (Pigott & Shapiro 1984; Goode & Magill 1986; Porretta 1988; Boyce & Del Rey 1990; Wrisberg 1991; Wrisberg & Liu 1991; Hall et al. 1994; Smith & Davies 1995; Goodwin & Meeuwse 1996; Farrow & Maschette 1997; Landin & Hebert 1997; Granda & Montilla 2003; Hwang 2003; Jackson 2006); whereas 11 studies included program variable practice (French et al. 1990; Bortoli et al. 1992; Hebert et al. 1996; Nair & Bunker 2000, 2002a, 2002b; Koufou et al. 2003; Ata 2005; Ata et al. 2005; Jones & French 2007; Zetou et al. 2007). An early study by Wulf (1988) contained both variations within and between generalized motor programs.

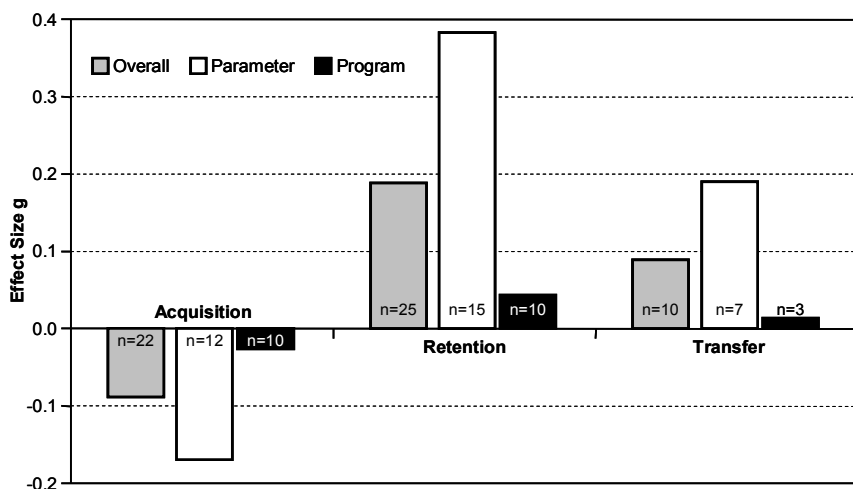


Fig. 2: Mean effect sizes for contextual interference effect in acquisition, retention and transfer of the 27 applied studies in the meta-analysis by Gelber (2005) separated in the overall effects as well as parameter and program variable practice effects

Nine out of the 12 studies related to dissimilar task variations found no significant advantages for random practice schedules either in retention or in transfer. Only the study by Ata et al. (2005) revealed a trend toward high contextual interference, in which two of the three skills to be learned showed significance in short-term retention; however, only one skill for long-term and none

of the three for transfer differed to lower contextual interference schedules. Two studies by Nair and Bunker (2000, 2002b) backed the idea of an optimal variability level, because schedules between blocked and random demonstrated significantly better contextual interference effects. Conversely, none of the 12 studies varying between motor programs verified significantly better results for variable practice in a blocked manner. Demonstrating no significant effect is not tantamount to there being no difference between the practice schedules; it could also be caused by too low test power or a too high beta error, respectively. This argument is invalidated by the low effect sizes throughout, indicating that in more complex tasks varying between quite different motor responses blocked practice was found to be as beneficial as random.

In contrast to studies involving various skills, most parameter variable studies contradict the Magill-and-Hall-hypothesis. Thirteen out of the 15 reviewed studies show at least partial, if not clear superiority, for high contextual interference. Moderate variability schedules outperformed blocked or random practice in two studies by Landin and Hebert (1997) and Pigott and Shapiro (1984), indicating again an inverted U-shaped contextual interference effect. Greater effect sizes for high amounts of contextual interference than mixed amounts could only be detected in lab-oriented research according to Brady's meta-analysis (2004).

Contrary to the negative contextual interference effect for acquisition performance in laboratory tasks, in applied complex settings 5 of the 26 studies showed even in the acquisition phase at least partially better results for high than for low contextual interference, as postulated in the differential learning approach. This was regardless of task variation type since three studies varied within the same motor program (Pigott & Shapiro 1984; Farrow & Maschette 1997; Smith & Davies 1995), whereas two were related to between program variations (Nair & Bunker 2000, 2002b).

Taking account of both inherent variability and introduced variability

The different contextual interference results between parameter and program variable practice in isolated laboratory and complex sport settings indicate the necessity for an optimal amount of movement variability, which is composed of the task inherent variability and the variability introduced through the exercises and their schedules.

If the level of noise or movement variability induced by the differential practice strategy in fact exceeds both that of parameter and program variable practice, as predefined by Schöllhorn et al. (2009b), such a level exceeds the optimal amount of noise even more. That is the case if inherent variability is not considered as well, because movement variability is furthermore affected by the subject's age, skill level and other moderator variables. Young and unskilled subjects innately or by definition have a high level of movement variability. Alike complex sport-related and open tasks are more variable than laboratory ones caused by the high number of degrees of freedom and the less predictable environmental conditions. In combination with a high amount of introduced variability by varying between different motor responses and in random order, the movement variability supposedly exceeds the optimal noise level and leads to an inferior learning performance (see Fig. 3).

In contrast, skilled adult subjects in closed laboratory tasks, varying between very similar motor responses in a low contextual interference schedule, may fall below the necessary amount of noise for best learning performance. Such a point-of-view is further supported by the consistent findings that in field-based research, adults gain more contextual interference effect than younger or less experienced learners (see Brady 2004, 2008). That is because for children or novices, random practice may result in too excessive response variability, as Wulf and Schmidt (1994) suggested earlier. Applied complex tasks, regardless of practicing program or parameter variations, seem to be sufficient contextual interference for young learners without the need for random practice. Therefore, blocked practice schedules should be preferred in early stages of skill learning and/or young subjects, as postulated by Hebert et al. (1996) and Wulf and Shea (2002).

An alternative not to exceed the optimal amount of variability in a random condition could be practicing variations, which differ less widely, especially within one skill. Conversely to applied contextual interference research, studies supporting the variability-of-practice hypothesis found that variable practice is more effective for children than for adults (cf. Schmidt & Lee 2011). What is commonly interpreted as a result of some lack of movement experiences in children could also be a consequence of a too low movement noise for adults, because most of those laboratory studies were conducted in a blocked practice sequence.

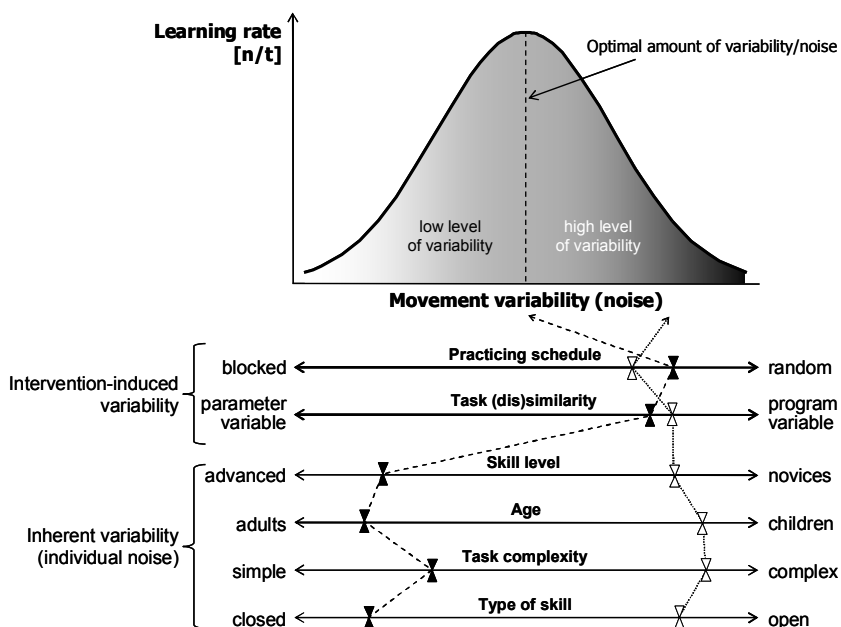


Fig. 3: Hypothesized optimal curve of motor learning as a function of movement variability (top); dependence of movement variability on different intervention-induced and inherent variability factors (bottom)

As Brady (2004, 2008) already urged, besides the moderating variables detected so far, upcoming meta-analytic studies should consider the number of skills and their magnitude of differences being taught. The emerged noise may not be easily considered as the sum of the magnitude of differences and their amount because highly diverging movements probably no longer interact with each other; therefore, they lead to reduced movement variability. Future meta-analyses might investigate moderating variables according to their inherent or introduced variability, and their interaction in order to find the right boundary or mediating conditions for the optimum of noise, if it indeed exists.

2.2 A couple of attempted explanations

A variety of theoretical explanations have been provided to elucidate the contextual interference effect including the impact of moderator variables being

detected. Most of them are based on the cognitive-psychological perspective of motor learning, and although they appear as rivaling theories, they are not mutually exclusive (cf. Lee & Simon 2004). Brady brought the different theories in his extensive 1998 review to a common denominator, which may be the enhanced cognitive activity, or the more effortful processing engendered by high interference schedules, and the deficient or decreased processing load as a consequence of low interference practice.

The predominant theoretical accounts involve the elaboration, reconstruction, pro- and retroactive interference, feedback usefulness, appropriate transfer, self-efficacy and motivational hypothesis.

Based on the theoretical explanation of the contextual interference effect in cognitive learning by William Battig (1966, 1972), and primarily supported by research concerning explicit memory tests, the elaboration-and-distinctiveness hypothesis by Shea and Morgan (1979) proposes that random practice in opposition to blocked practice necessitates comparative and contrastive analyses of the variations to be performed. Through higher variability within practice schedule, different task variations remain together in working memory and thereby enable an enhanced comparison and increased distinctiveness between tasks. Due to alterations between different encoding strategies, the demand on memory processing leads to worse acquisition, but improved retention performance and enables the learners to adapt more accurately to novel situations during transfer test being able to identify the relevant task features.

The action-plan or forgetting-and-reconstruction hypothesis provided by Lee and Magill (1983, 1985) is linked to the forgetting-helps-remembering paradox early revealed on the spacing effect by Cuddy and Jacoby (1982). Because random practice promotes forgetting of the previous trial, for the subsequent trial the action plan traditionally referred to motor program or parameter modification needs to be reconstructed. As the previously executed movement is no longer available in working memory, random practice engages more actively in problem-solving activity, weakening acquisition, but strengthening retention and transfer performance. The distinction between the elaboration and reconstruction views deals with working memory. While the first approach proposes the concurrent presence of more than one movement pattern in working memory facilitating comparison and contrast, the latter view empha-

sises the loss of information from working memory enforcing the movement to be newly generated. Lee and Simon (2004) consider contextual interference effect as an instance of spacing effect; that is, in random practice, individual trials are differently spaced compared to those in blocked practice as the latter is more massed than random practice.

Another noteworthy attempt to interpret contextual interference effect is the so-called retroactive and proactive interference or inhibition theory again derived from cognitive learning literature. This explanation emphasizes the disadvantage of blocked practice conditions, in which repeated practicing of one task retroactively interferes with the previously practiced tasks, or proactively interferes with and inhibits the recall of the consecutive ones, respectively, when they are tested later on in retention (cf. Magill & Hall 1990). It is assumed that, in contrast to blocked practice, random practice interferes less negatively with earlier or later practice trials because they are all consistently practiced throughout acquisition.

Wulf and Schmidt (1994) accentuate the unequal utilization of feedback in different contextual interference schedules. The basic idea refers to the less useful feedback of a task for the following one in random practice. As extended laboratory research has demonstrated, reduced feedback may enhance learning, especially when learners are more experienced (cf. Schmidt & Lee 2011 Wulf 2007). In contrast to simple skills, the learning of more complex sport skills does not benefit from reduced feedback frequencies (Wulf & Shea 2002), which could also account for the different findings of the contextual interference effect in laboratory and applied studies.

A further interpretation of the contextual interference effect places special emphasis on the similarity of the underlying processes between acquisition and transfer, which was brought forward by Lee (1988) as transfer-appropriate-processing hypothesis. Against the specificity hypothesis, neither the internal nor the external environmental conditions have to be similar, but more importantly the same problem-solving process is activated, i.e. probably the ability to adapt adequately to new situations. This comes very close to the objective of the differential learning approach, but raises the question if, in the context of explaining the contextual interference effect, it is not circularly argued (cf. Wiemeyer 1998).

From a pedagogical point of view, Vickers (1994) put additional factors into consideration of the contextual interference effect. Blocked practice is seen as a bottom-up strategy, in which the instructors predominantly manage the learning process by continually facilitating and supporting the learners. With regard to Gestalt psychology, random practice is thought of as a top-down strategy with the view to lead learners to perceive the whole skill, that in turn, stress learners' individual problem solving with less teacher feedback. Because less dependency on instructors is expected, and different levels of task complexity are experienced, random practice is advantageous in retention and transfer tests. A further aspect of Vicker's view is the false self-efficacy gained through acquisition in blocked practice. In retention and transfer, blocked practice learners feel self-doubt, frustration and unexpected failure, because they are less prepared than random learners for unfamiliar situations. Besides self-efficacy, Wulf et al. (1996) mentioned another emotional aspect, which could impact the contextual interference effect to some extent. In their motivational hypotheses random practice is, because of its diversified schedule character, simply more interesting. The higher motivational level results in a benefit for motor learning when practice trials are randomized, but cannot account for acquisition deficits.

As Wulf and Shea (2002) and Lee and Simon (2004) stated earlier, each of the briefly described theories and positions could, to some degree, reasonably elucidate the effect of contextual interference. However, they are unable to completely explain this phenomenon, and none of them is able to incorporate all the various influences of the above-quoted moderator variables. Regardless of the scientific evidence for each hypothesis, up to now no behavioral experiment has been conducted that provides strict evidence for a particular theory and concurrently allows the elimination of other explanations. This may be caused by the fact that only a few experimental settings afford an opportunity to directly contrast the different predictions (cf. Schmidt & Lee 2011). It may well be that the contextual interference phenomenon reflects an integrative approach involving a complex interactions between cognitive, motor, emotional, motivational and volitional factors (cf. Wiemeyer 1998). However, the best empirical findings supporting theoretical explanations are given by recent non-invasive neurophysiological studies using functional magnetic resonance imaging (fMRI) and various forms of transcranial magnetic stimulation (TMS) during practice and recall and following practice, respectively.

2.3 Analyzing the neural basis by means of fMRI and TMS

In a recent neurophysiological study, Cross et al. (2007) examined the contextual interference effect for the first time with functional neuroimaging. When learning a novel four-element sequencing task, the neural activity of blocked or random practicing subjects was measured during both sequence preparation and movement execution. In the experimental procedure, similar to Imink and Wright (1998), the behavioral data displayed the typical reverse effect of contextual interference and confirmed the increased time needed to mentally rehearse and prepare the movement sequences when they are randomly practiced opposite to blocked. As learning took place, the between groups' converging preparation time came along with the recruitment of distinct brain regions during movement planning and execution. Nevertheless, in the last third of training the sequence preparation took comparable time between groups, the random one engaged greater activity of the left primary sensorimotor cortex and the left superior parietal cortex. The increased activity in those brain regions was interpreted by the authors as a more intense preparation of each movement, even though the time for preparation did not differ. The actual movement executions were accompanied with increased activity in superior and medial frontal gyrus in the random schedule, which is in line with prior evidence of fMRI and rTMS studies, where those regions are critically involved in switching motor responses between trials (cf. Cross et al. 2007). Although the group differences in retention performance were not unambiguously attributable to the distinct brain activity, it substantiated the common idea that the contextual interference effect may be caused by an enhanced activity of additional brain regions during practice, but does not favor any of the above mentioned hypotheses.

While the fMRI measurements in the study by Cross et al. were restricted to the training trials, Lin and colleagues (2011) most recently investigated the hemodynamic response during 2 days of practice of a similar sequence learning task, as well as during a retention test 3 days later. Moreover, paired-pulse TMS was applied to the primary motor cortex in order to assess intracortical excitability before and after each training day and test. Even though in place of the go/no-go paradigm functional imaging was based on a blocked design, which did not allow differentiation between action planning and execution, the fMRI findings strengthened Cross et al.'s results as the slower response times

of random practice involved enhanced neural activity in sensorimotor and pre-frontal regions during acquisition. The delayed retention test reflected the typical reverse effect of contextual interference in both the behavioral data and the blood-oxygen-level-dependent (BOLD) signal. Compared to the blocked condition, random practice resulted in shorter response times and reduced brain activation in regions which overlapped to a great extent with those that were more active during acquisition. The blocked-random difference of neural recruitment in the left superior frontal gyrus during practice even linearly correlated with the benefit of random practice on retention – a relationship which could only be assessed because of the used within-subject cross-over design. The interpretation that the increased cortical activity due to the higher temporal variability of random scheduling contributed to the formation of enhanced memory traces and efficient long-term retrieval was further substantiated by the greater short-term (changes within the same day) and long-term (manifested after retention) increases of the primary motor cortex excitability following random practice. Although the relative hemodynamic response in the primary motor cortex did not differ between high and low contextual interference, the therein observed larger short-term excitability changes attributed to an increased intracortical facilitation after random practice were related to a greater relative BOLD activity in the medial frontal and superior frontal regions and predictive of the learning benefits of a randomized trial order. Alike Cross et al.'s work (2007), the study demonstrated enhanced task-related neural activities and therewith associated short- and long-term neural changes as a consequence of random practice compared to a blocked structure of practice. Notwithstanding that the authors particularly argued toward a more intensive reconstruction and retrieval, neither study can rule out that the observed contextual interference effects are caused by greater elaborative encoding or some other theoretical explanations.

In a series of recent experiments, Lin and co-workers (Lin et al. 2008; Lin et al. 2009; Lin et al. 2010) applied single-pulse TMS – a technique shown to create a transient virtual brain lesion – during the post-feedback intertrial interval of a fast discrete tracking task. Results provide strong indication that repeatedly reconstructing the action plan might be beneficial, but is not sufficient to explain the benefit of random scheduling compared to low contextual interference. Instead, the findings give neurophysiological (probably currently the best) support that the learning benefit of random practice is at least par-

tially attributable to the more elaborate processing induced by higher temporal variability during practice. This is because non-focal suprathreshold TMS pulses supposed to perturb the motor cortex immediately after each trial increased the error during random practice of the lever arm task and diminished the learning benefit in the retention test, which is consistent with the elaboration-processing point-of-view. Unlike the prediction of the forgetting-reconstruction hypothesis, however, TMS centered over the primary motor cortex contralateral to the moving arm neither deteriorated performance during blocked practice nor significantly improved motor learning (Lin et al. 2008).

Even though these results were widely replicated by Lin et al. (2010) with a distinct group of participants and they do not completely support the reconstruction hypothesis, this does not reject the explanation that an encouraged action plan reconstruction also contributes to the contextual interference effect. It is also likely that TMS application over the sensorimotor region did not induce any enhanced action plan reconstruction, since task performance during blocked practice did not worsen, but actually improved. Perturbing other cortical regions such as more frontal areas, which are noted to be involved in executive control and action selection or switching between actions during motor tasks (Rushworth et al. 2004), might indeed have enforced the loss of information from working memory encouraging action plan reconstruction and in turn, learning. Despite the fact that TMS perturbation actually reduced the tracking error during practice in blocked order, both studies (Lin et al. 2008; Lin et al. 2010) showed at least a trend for improved learning compared to the blocked no-TMS condition. This is potentially because, rather than enhancing forgetting and reconstruction, TMS pulses during blocked practice might have necessitated a reallocation of attentional resources to the motor task (Lin et al. 2008).

However, the causal role of the primary motor cortex to benefit from practice conditions of high temporal variability for motor learning, which is in line with the fMRI data by Cross et al. (2007) and the excitability measures by Lin et al. (2011), was corroborated in a further experiment using a figure-eight TMS coil for a more focal cortical disruption. While suprathreshold TMS centered over the primary motor cortex, once again, impaired motor performance in the recall phase, neither sub-threshold TMS over the same area, nor suprathreshold TMS over the lateral premotor cortex or peripheral arm stimulation applied

constantly during the same post-feedback intertrial interval was found to affect the learning benefit of random practice. This finding should not be mistaken that there are no other brain regions responsible for the effects of different practice schedules on skill acquisition and motor learning; in fact, quite the opposite may be inferred from Cross et al.'s (2007) and Lin et al.'s (2011) neuroimaging data (see also below). It simply gave proof that, in addition to their known role in movement execution, neural circuits in the primary motor cortex (within a short intertrial interval) are critical for establishing long-term memory representation of fast preprogrammed arm movements under high interference conditions. To take a closer look at the functional role of the primary motor cortex as it is selective to random practice benefits, the performance data obtained in Lin et al. (2008) were reanalyzed by distinguishing between temporal and spatial characteristics of the movement accuracy (Lin et al. 2009). Because intertrial TMS pulses during random practice deterred learning of movement timing, but did not significantly affect movement amplitude, it was suggested that enhanced cortical motor activity induced by high temporal variability may preferentially process temporal rather than spatial parameters of the to-be-learned lever arm task. On the contrary, despite the fact that the spatial accuracy significantly improved across practice and a tendency toward a contextual interference effect was observed, it is also conceivable that the disturbed cortical regions were less tuned to processing movement amplitude because the behavioral requirement for the chosen task might predominantly optimize movement timing: particularly in regard to the fact that cortical motor regions have been associated with planning, adjusting and encoding of task-specific spatial information (Lin et al. 2009).

That the neural substrates for long-term motor memory are differently modulated by the temporal variability of the practice structure is further substantiated by a post-training virtual lesion approach (Kantak et al. 2010; Tanaka et al. 2010). However, in comparison to single-pulse TMS applied between practice trials, focal 1-Hz repetitive TMS inducing a longer-lasting down-regulation in cortical activity after the end of the practice phase led to quite different effects on schedule-dependent memory stabilization. It suggests, at least partially, distinct mechanisms between motor memory encoding during practice and consolidation immediately after practice. That is, after post-practice TMS over the contralateral primary motor cortex, neither Kantak et al. (2010) using the same motor task as Lee and colleagues (Lin et al. 2008; Lin et al. 2010)

nor Tanaka et al. (2010) using a sequential visuomotor task similar to that described by Shea and Morgan (1979) observed an attenuation of the learning benefit through random scheduling. In contrast to Lee et al.'s finding, a virtual lesion of the same cortical region after constant practice of the lever arm task significantly deteriorated the recall performance (Kantak et al. 2010). Since the use of a distinct motor task by Tanaka et al. again resulted in a divergent effect of repetitive TMS following blocked practice, the involvement of neural circuits within the primary motor cortex seemed to be schedule-dependent and task-dependent, as well as temporal specific for the formation and stabilization of motor long-term memory.

Beyond the potential role of the primary motor cortex, Kantak et al. (2010) additionally disturbed the dorsolateral-prefrontal area both after constant practice of one criterion target and after practicing four different target position-time traces in a pseudo-randomized order. Conversely to the primary motor cortex, repetitive TMS following repeated practice of the same target trajectory did not alter motor skill retention, while after variable, random practice performance stabilization from the end of acquisition to retention was significantly attenuated. Control experiments in which TMS interference was not applied until 4 hours after end of practice affirmed that the effects of the virtual lesion – both the causal role of the primary motor cortex for constant practice and of the dorsolateral-prefrontal cortex for random practice – were temporally specific to the immediate post-training consolidation phase and were not the result of an effect on later recall or on the motor memory offline motor skill stabilization itself. The crucial involvement of the prefrontal regions under a high contextual interference supports the notion that working memory, action selection, and planning are more engaged than in practice regimes with lower temporal variability, and therefore, rely on higher-order motor areas (with the restriction that no sham TMS condition controlled for auditory clicking noise and the pressure of the TMS coil). This observation is well in line with the fMRI data by Cross et al. (2007) and Lin et al. (2011) as prefrontal regions showed greater relative BOLD activity and were even correlated with the learning benefits of random practice (see above), as well as consistent with simulations by artificial neural networks: in particular the hybrid multiple-level approach by Shea and Graf (1994) modeling different levels of information processing (for details see Chap. 3.3.11.3). The supplementary motor area is a further anatomical structure that was identified by Tanaka et al. (2010) to differentially

contribute to motor memory consolidation depending on the practice schedule. In contrast to the dorsal premotor cortex and a control region in the parietal lobe, post-training TMS over the supplementary motor cortex reduced recall relative to sham only in the blocked practice group. On the other hand, disruptive effects on consolidation were found neither when randomly practicing nor when TMS was applied 6 hours after training, or in an untrained non-sequential motor task (controlling for the specificity to the newly learned sequential skill). Since the supplementary motor area is known to play a contributory role in execution and learning of sequential movements, it is supposed that highly temporal variable practice may encourage a rapider and firmer storage of motor memories in this cortical region, which is then more resistant to physiological interference than lower varying trial orders, or, alternatively, drives them to become functionally independent of the supplementary motor cortex before the onset of repetitive TMS (Tanaka et al. 2010).

By the use of recent neuroimaging and TMS measurements to unveil the neural basis, and therewith to corroborate an explanation of the contextual interference effect, the neurophysiological approach thus far has failed to yield consistent results or an unambiguous interpretation. Overall, however, it has been demonstrated that the level and/or site of neural activity is crucially influenced by the temporal variability of the practice structure. This, of course, is a self-evident prediction, since high and low contextual interference has been widely shown to affect motor memory differentially on behavioral level, and the formation and maintenance of motor memory, in turn, is based on experience-dependent neural activity (see Chap. 3.3.2.1). Notwithstanding experimental limitations including behavioral aspects such as the simplicity of the chosen tasks, the small amount of practice and short retention intervals (as well as other variables known to moderate the contextual interference effect) and limitations of the used fMR and TMS methods such as the possible influence of the control conditions and the inaccuracy or the ambiguous causality between hemodynamic responses and neural activity (recently stated by Sirotin and Das in 2009), as well as the unambiguous consequences of the virtual lesion approach and its relatively small spatial resolution (cf. Perez et al. 2007), the just recently upcoming neurophysiological approach is undoubtedly a step forward to decode the mechanisms underlying cognitive and motor learning phenomena as contextual interference or differential learning, and underpinning variable practice.

3 The Differential Teaching and Learning Approach

In several studies, the differential learning approach was compared to traditional training approaches, including predominantly repetition learning or learning by means of a methodical series of exercises with error correction. The objective of those training studies, almost all conducted by Schöllhorn and colleagues, was the improvement of complex, sports related movement skills, containing forearm and overhand pass (Römer et al. 2003; Schöllhorn et al. 2006b); service (Burger 2006) and jumping (Spratte et al. 2007) in volleyball; shooting (Trockel & Schöllhorn 2003) and passing in soccer (Schöllhorn et al. 2006a); service in tennis (Humpert & Schöllhorn 2006) with mental training during retention (Schöllhorn et al. 2007d); free throwing in basketball (Schönherr & Schöllhorn 2003); starting in speed skating (Savelsbergh et al. 2010); jump shot (Pfeiffer & Jaitner 2003) and throwing strength (Pfeiffer et al. 2006) in team handball; push and flick in indoor hockey (Beckmann et al. 2010); shot put (Beckmann & Schöllhorn 2003); sit-and-reach and high jump (Schöllhorn et al. 2007e; Schöllhorn et al. 2009c); sprint hurdling over three (Jaitner et al. 2003) and five hurdles (Schöllhorn et al. 2010b); flat sprinting (Schöllhorn et al. 2001) and long-distance running (Simon et al. 2003); sprinting, one-leg hops and standing long jump (Beckmann & Gotzes 2009) and high jump (Denno et al. 2008) in physical education; as well as horse dressage riding (Ulm et al. 2007); quasi-static balance (Michelbrink & Schöllhorn 2005) and dynamic balance in bike riding (Schöllhorn et al. 2008c); and push-ups in aerobic gymnastics (Torrents & Balagué 2010). Recently, differential learning was also successfully applied to fine-motor skills such as handwriting (Vehof et al. 2009). In all of these studies, differential learning showed at least equal, if not superior, improvement in performance.

Against this background, it is not surprising that the differential learning approach is appreciated by Schöllhorn et al. (2009b) as the practicing strategy with the highest learning rate, although or rather because of the largest amount of induced noise. However, it should be taken into consideration that up to now there has been no direct comparison between differential learning and any other strategy of variable practice.

Differential learning results from the integration of several theoretical approaches to movement variability into a practical application for motor learning. All these approaches, some originated in distinct mother sciences, share the view that movement variability, or noise, is no longer associated with performance decrements or pathology; rather it is interpreted to be the opposite, as a deterministic and system inherent phenomenon necessary for adaptation and learning. The fundamental pillars on which the differential approach is built include the dynamical system concepts of synergetics and coordination dynamics; new methods for time series analysis; the concept of stochastic resonance; and insights derived from physiological and computational neuroscience.

3.1 Synergetics and coordination dynamics

Three decades ago, in 1984, J. A. Scott Kelso published his seminal and wide-ranging observations on rhythmic bimanual finger oscillations. Essentially influenced by Hermann Haken's synergetical postulations in the inanimate nature of physics, this was the starting point of a new research perspective in motor science known as "coordination dynamics". It is based on the concepts, methods, and tools investigating non-linear self-organizing systems in order to identify general laws of pattern formation. Coordination dynamics comprises a theory and a research program aiming to describe, explain and predict how coordination patterns form, persist, adapt, and change in different kinds of system at different levels of description (Kelso 2003; Jirsa & Kelso 2004).

One cornerstone of this approach is the study of non-equilibrium phase transitions, or order-order transitions, the qualitative change of the system's macroscopic behavior emerging self-organized without a central controller solely as a result of the system's dynamics (such as the horse's transition from trotting to galloping, if the velocity of locomotion increases as was first imagined by Haken). Non-equilibrium phase transitions are characterized by discontinuous (abrupt) and spontaneous jumps between different states of a system, or within the motor system between different coordinative modes brought about by parametric influences. Discontinuous transitions could be separated from continuous ones as instabilities occur before the transition point (cf. Van Emmerik & Van Wegen 2000).

Evidence for non-equilibrium phase transitions and their accompanying phenomena has been provided on different time scales and across a broad range of contexts concerning inanimate and animate nature. Beyond phase transitions in physics and chemistry, they have been observed on short time scale in cyclic and acyclic movements; postural coordination; visual and acoustic perception; language production and perception; and social (interpersonal) coordination; as well as in genetics, diseases and several movement disorders. Further observations have been made on medium time scale for motor and perceptual learning. On an even longer time scale, emerging phase transitions were part of the dynamic system's approach in developmental psychology and psychotherapy (for more details see Chap. 3.1.5.2). Such transitions, together with other key features like critical fluctuations and slowing down; bifurcation and symmetry breaking; hysteresis, bi- and multi-stability; intermittency; and sensitivity to initial conditions among others, are classic hallmarks of self-organizing systems.

Increasing variability, or more technically, fluctuations, especially critical ones that by definition accompany instabilities, are in the context of differential learning of particular importance because they are crucial to behavioral switches from one system's state to another. In the dynamical system approach, particularly in synergetics, behavioral variability or fluctuations are considered to be the essential precursor of change. Therefore, a general prediction of non-equilibrium phase transition is that fluctuations are markedly increased just as the dynamic complexities are enhanced when the transition is approached (Aramakiet al. 2006; Haken & Schiepek 2006; Hayes et al. 2007; Kelso 1995; Jantzen et al. 2008; Schiepek 2003; Scholz & Kelso 1989; Schöner & Kelso 1988; Thelen & Smith 1995; Van Geert & Van Dijk 2002). If such fluctuations exceed a certain value (anomalous variance) as the system becomes critically instable, it shifts into a new behavioral state.

It is a central message, or at least an assumption, from research in synergetics and coordination dynamics that variability within individuals is a necessary ingredient; a cause or condition for change – not only an accompanying phenomenon (Van der Maas & Hopkins 1998; Van Emmerik & Van Wegen 2000; Van Geert & Van Dijk 2002). Similar to the “Darwinian” principles of variation and selection, the enlarged variability prior to phase transitions offers flexibility as “the system is free to explore new and more adaptive associations and con-

figurations" (Thelen & Smith 1995, p. 145). Variability, as it is decisive in driving the system away from its current macroscopic state, points at a possible adaptive strategy instead of attributing it to measurement error or unwanted noise as was done in classical physics or information-processing theories (cf. Van der Maas & Hopkins 1998; Van Geert & Van Dijk 2002).

A recent and indicative example that a relationship between critical fluctuations and transitions in human system's states, even on a relatively large time scale, in fact exists was found in psychotherapy by Schiepek and co-workers (Schiepek 2003; Haken & Schiepek 2006; Schiepek & Perltitz 2009). In the analysis of the time series data produced by 91 inpatients with different mental disorders through self-ratings of psychotherapy processes, they found salient correlations between the local maxima of critical fluctuations and the therapy outcome (for more details see Chap. 3.1.5.2). Although an asserted relationship does not reveal an attribution of cause and effect, critical fluctuations are seen to reflect an increasing probability of transitions, and are therefore used for identification of periods in which the system could easier be changed (Haken & Schiepek 2006; Hayes et al. 2007). In contrast to just monitoring critical fluctuations to recognize appropriate time windows for interventions in order to bring about transitions, the approach of differential learning attempts to facilitate transitions in the motor system due to enhanced variability by most versatile exercises (cf. Schöllhorn 2000).

3.1.1 Synergetic principles derived from inanimate nature

Dynamical system theories like chaos theory, synergetics or dynamicism established in the middle of the last century, and since then gained increasing popularity, also had great impact on motor science and fruitful conceptual outcomes such as coordination dynamics. The interdisciplinary dynamic systems approach deals with open, dissipative complex systems, which are far from thermodynamic equilibrium and form patterns without a central control, i.e. in a self-organized manner. Complex dynamical systems inhere fundamental attributes separating them from simple and static ones, including among others the vast amount of freely varying component parts leading to a large number of redundant degrees of freedom, the non-linear interaction of subsystem components on different macro- and microscopic levels constraining the behavior of other subsystems, and the ability for self-organized emergence of

stable and unstable pattern, as well as their transitions (cf. Handford et al. 1997). Thus, non-linearity means a disproportional relationship between sensitive changes of initial conditions and behavioral output or even a shift into an entirely new kind of system state. Although dynamic systems are complex and non-linear, they are non-random; rather, they are globally deterministic (Thelen 1992). A paradigmatic example of an open non-linear system in which new patterns emerge self-organized from the interaction of many heterogeneous forces, often referred to as the most complex system of all, is the human brain to whose modeling Herrmann Haken, founder of the synergetic approach, early transferred synergetic principles (Schiepek & Perltitz 2009; Van Geert 1998).

Inspired by the emergence of coherent light field of the laser and the formation of convection pattern in fluid dynamics, both being systems that run through non-equilibrium phase transitions, Haken and collaborators laid down principles of self-organization. Opposing to continuous phase transitions, which are parametric, more or less smooth and can occur over a larger interval of control parameter values, non-linear phase transitions exhibit abrupt alterations of the system's qualitative behavior due to very small increments or decrements in the control parameter. Such parameters act as boundary conditions, and by definition move the system through different qualitative states, though not directly specifying those states. Depending on the system's stability, preservation of the behavioral state is maintained for a wide range of control parameter values; however, at a certain critical value, patterns form or change spontaneously accompanied by a dramatic reduction of the number of degrees of freedom. The so-called "slaving principle" offers the possibility to characterize the system's low-dimensional dynamics by a minimal set of collective variables or order parameters (Zanone & Kelso 1992a). In summary, it can be said that "a quantitative change of the control parameter gives rise to a qualitative change of the order parameter via a non-equilibrium phase transition" (Oullier & Jantzen 2008, p. 205f).

Apart from other phenomena that occurred in combination with discontinuous phase transitions such as hysteresis, intermittency, multi-stability, bifurcation, and symmetry breaking, the indicative loss of stability accompanies the phase shifts from one pattern to the other. The increasing instability in the transition region is reflected by increasing fluctuations. Although fluctuations are always present, their effects are non-linear, i.e. if fluctuations reach a critical level

(anomalous variance) the system's state is most likely to change into a new equilibrium-state given a certain level of noise. Therefore, the logical consequence is that an increase of variability pre-exceeds non-linear phase transitions and can be used as an indicator for the same. Along with that, a second applicable indicator for phase transitions is the so-called critical slowing down, wherein the system's behavior needs more time to recover from perturbations due to less stability in the transition region.

Both critical fluctuations and critical slowing down are fundamental characteristics of self-organizing systems (Van der Maas & Hopkins 1998) and have been demonstrated in a variety of processes of inanimate and animate nature. To name but a few common examples of non-parametric transitions between different stable states in physics and chemistry, one prototype is the transition from ordinary incoherent to coherent light field in the laser paradigm (Graham & Haken 1968), wherein electric current and coherent light waves were identified as control parameter and order parameter, respectively. The convection rolls of Rayleigh-Bénard (Bénard 1900; Rayleigh 1916; Malkus & Veronis 1958) can be described by the average convection velocity and are driven through their different pattern by the temperature gradient acting as control parameter like the angular velocity of the coaxial cylinder in the Taylor-Couette flow (Taylor 1923). In the chemical reaction of Belousov-Zhabotinsky (cf. Prigogine & Stengers 1984) it is the flow of different reactants or temperature that unspecifically constrains the different patterns emerging. Structural non-equilibrium phase transitions can be intricately observed in superconducting cuprates by ultrafast electron crystallography (Gedik et al. 2007). Using the chaotic pendulum (Stütz 1991), the Pohl's wheel (Haken 1995), or a video-feedback configuration (cf. Haken & Schiepek 2006), a non-linear transition from stable structured to unstructured chaotic patterns can be examined quite easily.

Independent of the material substance of the elements, the control parameter causes non-linear sequences of stability to instability to stability and of simplicity to complexity to simplicity, respectively, which captures the essence of dynamic systems (Thelen & Smith 1995). A common control parameter refers to the system's energy level, but in contrast to physical experiments in humans, the control parameters are generated and altered within the organism (Haken & Schiepek 2006).

3.1.2 Non-linear dynamics of rhythmic uni- and bimanual coordination

The appropriate selection of control and order parameter, as well as the applications of the synergetic principles and strategy in animate nature, was achieved by the coordination dynamics approach of J. A. Scott Kelso and colleagues based on their seminal rhythmic bimanual finger task (1984). Coordination dynamics is a theoretical and empirical approach aiming to elucidate how patterns of coordination emerge, change or disappear, and by which conditions such pattern formation is constrained in order to determine principles, laws and mechanisms of coordination (Jantzen et al. 2008; Jirsa & Kelso 2004; Kelso 2003). In addition to detailed observations of non-equilibrium phase transitions in bimanual coordination, cognitive or informational contributions like attending; perceiving; deciding; acting; learning; and remembering were investigated, and by making use of new imaging technologies, neurophysiological correlates were identified (Kelso 2003).

The successful modeling of coordinated finger movements through two coupled oscillators by Haken et al. (1985) and its progression has generated an astounding amount of subsequent research, and not only in motor science. Although, or precisely because, the rhythmic movement paradigm contains a relatively simple movement, as only few muscles and reactive forces are involved, it allows a rather simple mathematical description of the movement system's dynamics by means of relative phase as order parameter and movement speed as a key control parameter. Another advantage is that it provides only a small number of stationary phase states and transitions in between these states (Jirsa & Kelso 2004).

As it is commonly known that when the rate of two in parallel (anti-phase) mode oscillating index fingers is gradually increased, a spontaneous non-linear transition to symmetrical (in-phase) oscillations occurs at a critical movement frequency. Such phase transitions accompanying bimanual phenomena are sensitive to musculoskeletal, informational and intentional factors, depend on individual pre-experiences and may vary substantially across participants and experimental settings (cf. Jantzen et al. 2008). In order to quantitatively describe the qualitative behavior of the system, i.e. spatio-temporal relationship between the coordinated fingers, the discrete or continuous relative phase is used to represent both the position and velocity of the end effectors (for de-

tailed comparisons of qualitative and quantitative methods see Hamill et al. 2000 and Glazier et al. 2004).

The relative phase, brought into use in 1939 by Erich von Holst, is an abstract relationship of the interacting microscopic component subsystems that describes the coordination dynamics on a macroscopic scale, as it is the aim of collective variables in synergetics. Among other parameters, the relative phase became the most important order parameter in coordination dynamics research (Fuchs & Jirsa 2008). First measured by Kelso (published in the classical paper of 1984) and confirmed numerous times, the instability of the coordination pattern increased when the transition region is approached, as marked by the enhanced fluctuations of the relative phase accompanying the shift from anti-phase to in-phase mode. The increase in coordination pattern variability that typically precedes the transition points constitutes both a key feature of dynamical systems and the central message of coordination dynamics research, namely that "variability is a necessary ingredient for coordination change" (Van Emmerik & Van Wegen 2000, p. 401).

Three measurable parameters were used in the classical finger experiment to assess the loss of stability containing the variance, or standard deviation, of the relative phase time series, the local relaxation time following small perturbations, and the switching time (Scholz & Kelso 1989; Schöner & Kelso 1988). The amount of fluctuations, as measured by standard deviation of collective variable time series, reflects the strength of stochastic forces. According to Schöner and Kelso (1988), this source of noise inheres interacting coupled subsystems and acts as persistent perturbations producing deviations from the stable state. The local relaxation time refers to the synergetic principle of critical slowing down, describing the system's decrease of reaction time to external perturbations in the vicinity of critical regions. Applying a mechanical torque to one of the oscillating hands in the bimanual movement task, the relaxation time of such perturbations was estimated from the offset of perturbation until the movement pattern regains stability. The switching time was defined by Schöner and Kelso (1988) as the duration of the transient from loss of stability of the outgoing state to recovery of stability in the new state, wherein the time duration is again referred to the level of noise in the system.

Are the critical fluctuations entirely random?

It is an outstanding question whether increased fluctuations accompanying transition are randomly noisy and stochastic, or chaotic and deterministic, or perhaps a combination of both. In contrast to deterministic chaotic processes, random noise corresponds to white noise, which is in physics defined as random signal or process with a flat power spectral density, i.e. the signal's power is equally distributed within a fixed bandwidth (see also Chap. 3.2.2.2). In the relationship of behavioral data, noise can result out of several sources (cf. Thelen & Smith 1995). On the one hand, noise can be caused by systematic or unsystematic (white noise) errors in the data acquisition or analysis, which is as a matter of course, undesirable and should also be avoided in the system dynamics view. On the other hand, though the experimental settings would lead to consistent data, they could be still noisy reflecting chaotic and stochastic variability in the subject's performance. In coordination dynamics this type of variability displays the subject's regions and transitions of stable and unstable behavior constrained by the task requirements.

The original hypothesis of dynamical systems theory points to the assumption that critical instabilities occur due to collapsed pattern formation. Prior to a new coordinated pattern, the pre-existing pattern vanishes in order to make room for new symmetry states. This is attributed to an increased probability of random fluctuations emerging from internal properties or environmental conditions and influencing the system's behavior.

Schmidt and colleagues (Schmidt et al. 1991; Schmidt et al. 1993; Schmidt & Turvey 1995; for a summary see Riley & Turvey 2002) argued against attributing relative phase variability to additive randomness (cf. Schöner et al. 1986); they instead argued for a blend of deterministic and random components in rhythmic intersegmental coordination. The observed power in the frequency spectrum of the relative phase showed no flat distribution in case of random, white noise; rather, it revealed a type of colored noise with a negative power slope indicating deterministic influences on relative phase variability (Schmidt et al. 1993; Riley & Turvey 2002).

Simulations and experimental results by Riley et al. (2001) reconfirm the notion of both deterministic and random parts shaping relative phase variability during in- and anti-phase coordination of left- and right-hand-oscillated pendulums with different frequencies and pendulum lengths (causing different de-

degrees of cooperation and competition between component oscillator dynamics).

On a larger time scale, Haken and Schiepek (2006) analyzed time series of self-rated psychotherapy processes and found local correlation maxima of the 53 assessed items during order-to-order transitions indicated by the critical complexity index and recurrence plots (see Chap. 3.2.2.2). According to the authors, a simultaneous increase of system's dynamic coherence near transition points and increase of time series complexity provide an indication of macroscopic chaoticity rather than randomness. However, it is equally, if not more probable, that the resulting and observable critical fluctuations are caused by both chaotic and random forces.

3.1.2.1 Modeling coordination dynamics: the classic HKB model and its progression

Based on synergetics and non-linear oscillator theory, the behavioral dynamics of rhythmically bimanual finger movements was first theoretically modeled by Hermann Haken, J. A. Scott Kelso and Herbert Bunz in 1985, and since then have become well known as the HKB model of coordination. Both the steady states and phase transition behavior were explicated by a mathematical formalism in terms of two non-linearly coupled, non-linear oscillators that are self-sustained, i.e. not driven from the outside.

In order to reproduce the experimentally observed phenomena in bimanual coordination, a non-linear hybrid oscillator equation consisting of a van-der-Pol and Rayleigh terms was used. As related to the empirical data, both oscillators were non-linearly coupled resulting in a combination of differences in the locations and velocities of the individual components. The between-oscillator coupling can be thought of as two swinging pendulums connected by a non-linear spring (i.e. the force exerted by the spring onto the pendulum is not proportional to the difference in their location); however, the coupling is achieved via the nervous system. Therefore, the HKB model describes a complex system composed of the mechanical motions of the hands generated in large part by neuromuscular input (Haken et al. 1985).

In contrast to physics or chemistry, wherein the order parameters could be derived from basic laws of nature, the strategy for a minimal theoretical model in bimanual coordination had to be different because the laws guiding coordi-

nation or brain dynamics are a priori not known, and thus, cannot be determined through basic principles (Fuchs & Jirsa 2008). The HKB approach pursued a top-down rather than a bottom-up strategy, first developing a macroscopic description on the basis of an appropriate order parameter. Thereafter, such description can facilitate the search for the behavioral dynamic on a lower meso- or microscopic level. Both approaches to the HKB model, bottom-up and top-down, were introduced and compared by Fuchs and Jirsa (2008).

Increasing model accuracy by adding a random noise term

The original HKB model was extended to a time-dependent stochastic differential equation by Schöner et al. (1986) in order to analyze the system's fluctuational character at the level of the order parameter because fluctuations have a decisive role in initiating a transition between one state and the other at a critical value of the control parameter.

To account for the fluctuations present in the experimental data, a stochastic force in terms of a Gaussian white noise process with certain strength was added to the equation of motion. This was done by a transformation into a Fokker-Planck equation describing the time evolution of the probability distribution for a system described (cf. Kelso 1995). The rationale for the particular choice of such stochastic force was the assumption that stochastic properties do not depend qualitatively on the details of the dynamics of it near the transition, but the degrees of freedom adding noise to the system act on a time scale that is much faster than the time scale of the order parameter (Schöner et al. 1986).

By using experimental data of local relaxation time and measures of the relative phase variability in both coordination modes outside the transition region, numerous solutions for an estimation of the model parameters, including the noise strength in the system, were possible. The predictions of the theoretical model could be verified by Schöner and Kelso (1988) through the measured switching times between coordination patterns.

Modeling unimanual perception-action coordination by adding a symmetry breaking term

A further progression of the classic HKB model was achieved under the aspect of two oscillators with different eigenfrequencies; e.g. when coordinating an

arm and a leg, or in rhythmic unimanual perception-action patterns, as when one finger is coordinated in relation to a metronome.

To account for such differences, the original HKB equation was extended by linear term called symmetry breaking term, which is the difference between the two eigenfrequencies of the single oscillators in relation to the common frequency of the coupled system. A finite value for the symmetry breaking term leads to qualitative changes in the dynamical behavior of the relative phase and, as its name implies, leads to a break in the cyclic symmetry. The linear constant causes an additional slope in the HKB potential that, for small values, slightly shifts the fix points away from the pure in-phase and anti-phase mode. Thus, the transitions have a preferred direction when the control parameter exceeds the critical value. A further increase of the symmetry breaking term results in a loss of the stable fix points, i.e. the system is no longer phase locked (cf. Fuchs & Jirsa 2008; Kelso 1995).

The application of the theoretical model by Kelso et al. (1990) in the action-perception paradigm, synchronizing or syncopating finger flexion with an auditory metronome showed the predicted non-equilibrium phase transitions, as well as the expected loss of entrainment. In the action-perception case, the symmetry breaking term incorporates the intrinsic differences between the frequency that the moving limb generates spontaneously and the metronome frequency. Because any situation that creates differences between the interacting elements is a potential source of symmetry breaking, and because the metronome and limb are obviously different components, symmetry of the dynamics can no longer be assumed (cf. Kelso 1995).

Modeling bimanual perception-action coordination by adding a parametric driving term

Jirsa et al. (2000) put the action-perception paradigm forward to bimanual coordination by analytically and numerically studying the contribution of environmental information to coordination dynamics within the frame work of HKB modeling, which in its original form describes the self-paced intrinsic dynamics of the system. Their developed theoretical model accounts for the impact of a metronome on the limb's intrinsic dynamics at both collective and component levels in the paradigmatic case of bimanual coordination.

In previous experiments, it was shown that the synchronization of an effector with the environment – in literature, referred to as anchoring – leads to global coordinative consequences. It changes the stability and variability of the relative phase, the reversal point coincidence and the movement amplitude (cf. Fuchs & Jirsa 2008; Jirsa et al. 2000). Specific external information, such as a metronome to which one's action is synchronized, is able to stabilize the system's behavior that would otherwise be susceptible to switch to more stable modes of coordination; perhaps shifting the critical frequency to a higher one.

Jirsa et al. (2000) implemented a parametric driving term (also called stabilization term) in the HKB model reflecting the inextricable coupling between environmental information and the movement's dynamics in sensorimotor coordination. In the special case of non-coupling, the model reduces to the original HKB equation and preserves the main characteristics of the HKB model for bimanual coordination. In contrast to a linear term, the multiplicative coupling accounts for single limb and multi limb-metronome interaction at multiple frequency ratios between stimulus and movement.

Kelso et al. (2001) extended the sensorimotor coordination paradigm to haptic information within rhythmic unimanual flexion-extension movements paced to an auditory metronome. Phase transitions were studied in conditions without haptic contact, haptic contact at peak flexion and extension, when peak flexion was on or off beat, and haptic contact at both peak extension and flexion. While active touch stabilized coordination pattern when coincident with auditory metronome, haptic information destabilized coordination when it did not coincide with auditory input. The destabilization effect of non-coincident perceptual input may be caused by a multimodal conflict or neural interference between coordinating one phase of movement with sound and the other with touch, whereas the stabilizing effect of auditory and haptic coincidence probably results from neuronal integration into coherent action-perception unit (Kelso et al. 2001).

As expected, both visual input and eye movement also have a stabilizing effect on sensorimotor coordination, as demonstrated by Schmidt et al. (2007) who used unimanual swinging hand-held pendulums while visually tracking an oscillating stimulus, or keeping the eyes fixed on a stationary location.

Modeling multi-frequency bimanual coordination by a polynomial of coupling terms

In order to predict phenomena emerging from polyrhythmic performance in interlimb coordination, i.e. when the limbs did not oscillate at the same frequency, but oscillate at some multi-frequency relation, several theoretical models were elaborated in the frame work of a non-linear system of coupled oscillators. If two limbs have to be coordinated at different frequencies, some certain frequency ratios are performed with greater ease and stability than others. Results of empirical studies in bimanual multi-frequency tasks concluded that, in general, higher-order ratios with larger numerators and denominators are performed with larger variability than lower-order ratios, and are frequently attracted to lower-order ratios. Furthermore, since such transitions occurred more often at higher movement frequencies, they have a strong impact on the stability of the frequency locks. It was assumed that such frequency-ratio-dependent changes in stability originate from the changes in the coupling between them (Haken et al. 1996; Peper et al. 1995; Peper & Beek 1998, 1999).

On the basis of empirical results in interlimb coordination of skilled drummers (performing different frequency ratios while movement rate was gradually increased), Haken et al. (1996) formulated a theoretical model to predict the observed transition routes, which included the HKB model as a special case. In contrast to the sine circle map (a one-dimensional difference equation describing the influence of a periodic force on the phase of an oscillator and revealing regions of stable mode locking), which did not capture some observed transitions, the interaction function in the HPBD model consists of a polynomial of coupling terms that allow for specific frequency locks. The magnitudes of these coupling terms are related to both the amplitude of oscillation and the order of the frequency lock. Because movement frequency and amplitude are inversely related, the relative magnitudes of the coupling terms also were associated to the control parameter. Therefore, if movement frequency is increased, lower-order terms become more important than higher-order ones, leading to a loss of stability and to an attainment of lower-order frequency locks.

Such dependence of the degree of coupling on the movement amplitude was contradicted by experimental results of polyrhythmic tapping by Peper and

Beek (1998), in which the effects of amplitude and frequency were experimentally dissociated. While no effects of amplitude were observed, coupling strength and pattern stability showed an inverse relationship to movement frequency. These findings argue against an essential role of an inverse frequency-amplitude-relation in the neurophysiological processes of interlimb coordination, and thus against HKB and HPBD model, which both implicate this at the level of coupled oscillators (cf. Peper & Beek 1999).

Modeling rhythmic interlimb coordination by dissociating between neural effector dynamics

To overcome the shortcomings of the preceded HKB models that could not be remedied by simple changes in the oscillator or coupling parameters, Beek et al. (2002) chose a different modeling approach that replaces the amplitude coupling by a coupling function in which the effect of frequency on the stability of the relative phase is not mediated by movement amplitude.

To meet these demands, a two-tiered model for interlimb coordination was outlined in which four rather than two coupled oscillators, two each at the neural and at the effector level, were proposed (Beek et al. 2002). In the more encompassing model, both non-linear "neural" oscillators were bidirectionally coupled to the linear "effector" oscillators predicting the movements of each individual limb (for a detailed discussion in relation to empirical data see also Peper et al. 2004 and Ridderikhoff et al. 2004).

Despite the drawback of introducing an entire level of dynamics and corresponding events that are not readily accessible by measurements, the four-oscillator model substantially increased the explanatory power by making the explicit dissociation between the neural dynamics and the effector dynamics (Ridderikhoff et al. 2004). It accounts for the known stability properties of relative phase, whereas the decrease of amplitude in the oscillating limbs is treated principally as a peripheral effect (Beek et al. 2002). Because the HKB model did not differentiate between neurophysiological, muscular or biomechanical aspects, it is constrained by its phenomenological character. The two-tiered model links the observed stability characteristics in a more natural framework to more specific aspects of the movement system, such as the underlying neurophysiological processes (Ridderikhoff et al. 2004).

3.1.2.2 Central neural correlates of relative phase dynamics

The coordination dynamics approach – its principles of self-organization, its empirical results and its modelings – had great impact on neuroscience by providing a new perspective of understanding the brain and its underlying functions. Inversely, brain sciences – especially by their sophisticated imaging technologies and analyzing methods – had a similar influence on coordination dynamics forming the basis to gain insights on how the component subsystems interact on a mesoscopic level during pattern formation and vanishing processes.

In order to reveal the contribution of the central neural activity on the full coordination dynamics, the neurophysiological correlates of the behavioral dynamics were investigated by isolating specific features of coordination (Oullier & Jantzen 2008). Beyond the comparison of more or less stable and instable patterns, in recent studies neurophysiological substrates of phase transitions accompanying phenomena could be identified by the use of high time resolution devices. After the elementary magnetoencephalographic (MEG) investigations by Kelso and colleagues in the early 90s, advanced technologies like TMS and event-related fMRI enables the relation of enhanced behavioral fluctuations to the activity of the central nervous system.

In general, the findings of coordination dynamics on neural indices support the initial thesis of metastability as a principle of behavioral and brain function (Jantzen et al. 2008). The brain, constrained by the biomechanical and neuromuscular effector systems, as well as the perceived and intended information, acts as a pattern-forming system being able to switch flexibly between coherent states. This flexible switching on an action or cognition corresponding time scale rests upon the simultaneous ability of diverse brain regions to function autonomously and in concert at the same time (Jantzen et al. 2008). The body of work concerning sensorimotor coordination underlines the suggestion that the movement behavior and the underlying cortical processes share similar dynamics (Oullier & Jantzen 2008).

Measurement tools and coordination paradigms

To estimate the intensity of the brain's neural activity and its location, a number of different imaging tools with diverse temporal and spatial resolutions, mostly inversely related, were used. The imaging techniques for the detection

of neural indices underlying coordination dynamics comprise MEG with different sensor types and arrays, such as the superconducting quantum interference device (Bassett et al. 2006; Daffertshofer et al. 2000; Fuchs et al. 1992; Fuchs et al. 2000; Haken & Schiepek 2006; Jantzen et al. 2001; Kelso et al. 1992; Kelso et al. 1998; Kowalik et al., as cited in Haken & Schiepek 2006); electroencephalography (Tognoli 2008); unilateral or central, and graded or repetitive transcranial magnetic stimulation (Chen et al. 2005; Meyer-Lindenberg et al. 2002; Steyvers et al. 2003); positron emission tomography (Meyer-Lindenberg et al. 2002); functional magnetic resonance imaging (fMRI: Debaere et al. 2004; Jantzen & Kelso 2007; Jantzen et al. 2002, 2004; Mayville et al. 2002; Nair et al. 2003; Nair et al. 2005; Oullier et al. 2003, as cited in Oullier & Jantzen 2008; Oullier et al. 2005a & 2005b; Oullier et al. 2006; Oullier & Jantzen 2008); and event-related fMRI (Aramaki et al. 2006; Jantzen et al. 2008); as well as combined applications.

Due to established knowledge of the dynamics of classical finger oscillating movements, these coordination patterns and their phase shifts were primarily studied, whereby sport-related gross-motor skills are excluded because of the constraints of the measurement systems. Beyond the majority of studies focusing on the syncopation-synchronization paradigm such as single-finger, finger-to-thumb opposition and bimanual movements in relation to an auditory or visual metronome (Daffertshofer et al. 2000; Fuchs et al. 1992; Fuchs et al. 2000; Jantzen & Kelso 2007; Jantzen et al. 2004; Kelso et al. 1992; Kelso et al. 1998; Bassett et al. 2006; Mayville et al. 2002; Oullier et al. 2003, as cited in Oullier & Jantzen 2008; Oullier et al. 2005; Oullier et al. 2006), typical rhythmic bimanual finger movements with constant or increasing movement rates (Aramaki et al. 2006; Chen et al. 2005; Jantzen et al. 2008; Meyer-Lindenberg et al. 2002; Nair et al. 2003; Nair et al. 2005; Steyvers et al. 2003) were investigated. Further observations on a short time scale, including imagined versus physically executed coordination patterns (Nair et al. 2003; Nair et al. 2005; Oullier et al. 2005a & 2005b), as well as interpersonal coordination (Tognoli 2008) and movement disorders (Nair et al. 2005) were analyzed. On a longer time scale, Jantzen et al. (2001) used MEG, and Jantzen et al. (2002) and Debaere et al. (2004) applied fMRI measurements to study neurophysiological correlates of learning processes. As early as 1996 and 1997, Jirsa and Haken tried to model the neural dynamics of synchronized and syncopated movements recorded by MEG.

Phase transitions in central neural activity: first evidence by MEG studies

In order to uncover the link between the dynamics of behavior and brain, by connecting these levels through their shared dynamics, Kelso, Fuchs and colleagues (Fuchs et al. 1992; Kelso et al. 1992) used very sensitive magnetometers, called "superconducting quantum interference device(s)" (SQUID), measuring extremely small magnetic fields during syncopation of two consecutive auditory stimuli. The classical ramping paradigm used enabled the observation of phase shift phenomena in both behavior and neural activity.

Although the MEG device used at that time is not comparable to the present one, qualitative changes at critical control parameter values could be observed not only in behavior but also in brain activity. That is, fluctuations also increased in neuromagnetic activity during phase transitions, even though the SQUID data, in relation to the behavioral ones, as a whole were noisier. Critical slowing down, an additional indicator for the approach toward transition point and increased instability, was evident in the brain activity because of the prolonged times for returning to pre-perturbation activity. Both critical fluctuations and slowing down indicate the enhanced susceptibility of the brain to switch flexibly from one coherent state to another (Kelso 1995).

It is the synergetic "slaving" principle that predicts the reduction of the degrees of freedom near instability points, which provides the possibility of describing even complex systems by only few collective variables. This principle could also be outlined for the description of brain dynamics by capturing the macroscopic spatio-temporal brain behavior using the Karhunen-Loève expansion for decomposition of SQUID sensors' signals. Thereby, it was possible to principally characterize the spatio-temporal dynamics by only two out of 14 identified spatial modes (Kelso 1995).

The comparison of the brain's magnetic field between pre- and post-transition revealed an amplitude decrease (even though the movement rate is higher) and less coherent activity during synchronization (even though this pattern is more stable) accompanied by a phase shift in certain sensors. The spectral power analyses of several SQUIDS resulted in doubling to tripling of the stimulus-response frequency, which could not be repeated in a case study of Daffertshofer et al. (2000) who used sizably larger SQUID arrays: however, was reconfirmed by Fuchs et al. (2000) across different subjects (differences may

have occurred due to different experimental setups, i.e. subject's eyes closed or open).

Another MEG study by Kowalik et al. (as cited in Haken & Schiepek 2006) could emphasize the salutatory increase of fluctuations in neuromagnetic activity during frequency induced bimanual finger movements from anti- to in-phase mode. The increased chaosticity in bilateral premotor areas was determined by the largest local Lyapunov exponent.

Comparing stabile and instable coordination modes by means of PET and TMS

A different kind of approach used to demonstrate the decreasing stability in the neighborhood of qualitative behavioral changes, even on a neural level, was elaborated by Meyer-Lindenberg et al. (2002) in a highly recognized experiment (for a review see also Meyer-Lindenberg & Bassett 2008). During performance of continuous repetitive bimanual index finger movements, both in in-phase and anti-phase modes, at four different frequencies below, yet near the critical value, the regional cerebral blood flow (rCBF) was measured through positron emission tomography (PET).

Because it is commonly accepted that changes in rCBF accompany synaptic firing, cortical regions were mapped out in order to identify areas whose activities are related to the degree of behavioral instability. This instability was correlated to increased rCBF across a frontal motor network including supplementary motor (SMA) and bilateral premotor (PMA) cortices. Located over those and other regions, graded TMS was used to transiently disturb neural activity during instructed movement patterns predicting that the neural perturbation should differently affect stable and instable patterns and may cause shifts from the less stable to the stable pattern but not the reverse. These predicted transitions were verified primarily by TMS pulse over PMA and SMA, whereby the TMS intensity and movement rate interacted in such a way that the highest transition probability was achieved when the pattern stability was less and the degree of neural disturbance was high. Although the experimental conditions were held constant, it was observed in repeated trials of TMS that behavioral transitions occurred at times, and at times they did not; that is, under the same stimulus and movement parameters, even minimal changes in initial conditions could cause macroscopically differing neural consequences (Meyer-Lindenberg et al. 2002).

The different effects on behavioral stable and instable bimanual patterns through cortical TMS disturbance were further supported by Steyvers et al. (2003) without provoking phase transitions. In-phase and anti-phase finger movements near a cycling frequency, where anti-phase mode could only just be maintained, were neuronally disturbed by repetitive TMS over frontocentral cortical motor regions. Although no changes in the relative phase variability or movement duration and amplitude, neither in in-phase nor in anti-phase mode, could be detected (probably due to the already substantially high pre-stimulation variability), the mean relative phase error between hands increased, but only in the less stable anti-phase pattern.

Such impacts on the behavioral dynamics are missing at self-paced, comfortable movement rates because even the anti-phase dynamics is stable enough against unilateral TMS stimulation, as shown by Chen et al. (2005). By quantifying TMS interruption through predefined EMG-resetting index, in-phase co-ordination TMS pulses impacted both hands regardless of contra- or ipsilateral stimulation, whereby the latter showed even stronger effects, which indicates hemispheric coupling. The little effects on anti-phase mode were attributed by the authors to the more complicated communication between hemispheres working more independently after disruption.

Neural indices of behavioral (in)stability from event-related and blocked fMRI analyses

The progression in fMRI devices and analyzing tools, especially the improved temporal resolution, enables not only conventional block paradigms, but also event-related designs that are essential for the investigation of the neural mechanisms of spontaneous and intentional pattern switching because neural activity is attributable to key moments in coordination dynamics, such as the emergence of critical fluctuations, loss of pattern stability or pattern change processes (Jantzen et al. 2008).

Recently, Jantzen et al. (2008) explored the neural basis of pattern stability as a function of intentional switching by the use of the bimanual coordination paradigm. The blood oxygen level dependent (BOLD) signal linked to the hemodynamic response of neural activity was recorded at different movement frequencies during intentional switches from less stable anti-phase to more stable in-phase mode, or vice versa. The BOLD activity was found to be higher

during transitions from in-phase to anti-phase in diverse cortical and subcortical regions including pre-SMA and basal ganglia. Such key regions are thought to enable the transitions between behavioral states without necessarily participating in the processing within that particular state. These so-called behavioral catalysts may parameterize the intrinsic coordination dynamics, specifically, the relative stability of the behavioral patterns underlying intentional switches among patterns (Jantzen et al. 2008; McIntosh 2008).

Contrary to intentional pattern switches, the event-related fMRI study of Aramaki et al. (2006) investigated spontaneous transitions between bimanual finger tapping. Beginning each trial in anti-phase mode, subjects performed five different movement rates being below and above critical frequency in order to detect phase-transition and pattern related brain activity. The most important finding was that the transition-related activation map (mainly the prefrontal, premotor, and parietal regions) was clearly distinct from the pattern-mode-related activity of the motor execution areas (mainly the SMA proper and the dorsal PMA) with little overlap between state- and transition-related activation. The attempt to maintain the anti-phase-mode near transition regions can be viewed as the process of restoring temporal and spatial stability, which necessitates the activation of a parieto-premotor-prefrontal network considered to be responsible for motor planning or preparation (Aramaki et al. 2006).

In contrast to event-related designs, common fMRI studies were arranged in discrete blocks due to the weak temporal resolution by simply alternating coordination blocks with control conditions (Jantzen et al. 2008). Such an approach allows the comparison between patterns of different stability and its interaction with movement rate as it destabilizes less stable patterns with more stable ones, remaining hardly affected by rate when it increases. Most studies making use of this approach chose the syncopation-synchronization paradigm first conducted by Mayville et al. (2002), and since then replicated several times with unimanual finger tapping (Jantzen et al. 2004; Jantzen & Kelso 2007) and finger-to-thumb opposition movements (Mayville et al. 2002), or comparing both uni- and bimanual coordination patterns (Oullier et al. 2003) at one fixed or different movement rates.

Across studies, the comparison of syncopated versus synchronized movements revealed the consistent finding, regardless of whether coordination was uni- or bimanual, that not only greater neural activity, but also additional brain re-

gions are activated in the less stable, syncopated coordination pattern. Remarkably, no brain region was found to be less active during syncopation than synchronization. Predominantly premotor cortical regions, especially SMA, demonstrated both increased and extended BOLD signals during off-beat movements, wherein the cerebellum, basal ganglia, and prefrontal and temporal association cortices were also activated. Because SMA activity is seen in patterns that are more instable regardless of the components being coordinated, Oullier and Jantzen (2008) argue against the specific role of SMA in mediating bimanual coupling, but for the intrinsic pattern stability reflected by SMA activity. That is, as the organization and maintenance of pattern stability in less stable coordinated movements require growing demand for sensorimotor integration, neural activity may be enhanced and extended.

Mayville et al.'s interpretation (2002) of the different neural activation between and synchronization and syncopation was related to the enhanced efforts during preparation and monitoring of syncopated movements because they may be planned and executed individually on each perception-action cycle. The greater attentional demand may be based on the potential movement requirements, e.g. reacting to a stimulus, anticipating the following one, and timing the interstimulus interval (Oullier & Jantzen 2008). In opposition to this suggestion, Oullier et al. (2006) found indications that the syncopation and synchronization differences do reflect their distinct intrinsic pattern stability on neural level (internal representation) and are not solely governed by external stimulus. By experimentally dissociating between syncopation and reaction, neural activity could be clearly differentiated in regions that are attributable to working memory and response selection of stimulus-driven reaction movements.

Neural dynamics in the absence of real movements

A body of work demonstrated that stability and instability of a movement pattern are constrained and determined by their neuromuscular involvement; such as the form of a pan constrains and determines the kind of pattern emerging in the convection roll paradigm. However, the pattern's (in)stability is not imposed only by neuromuscular constraints involved as was revealed in a couple of new imaging studies that compared physically executed movement with merely imaging them. For example, in a functional MRI study by Oullier

et al. (2005a, 2005b), subjects performed synchronized and syncopated finger-to-thumb opposition movements at a fixed frequency. In addition, they simply imagined the same coordination patterns, perceiving the same sensory input (metronome) as during physical execution. The differences in neural activity between the more stable synchronization and the less stable syncopation pattern, stated in the premotor and supplementary motor, basal ganglia, and lateral cerebellar brain regions, persisted when the movements were only mentally and not physically performed. So, the intrinsic dynamics even exists in the absence of actual movement; therefore, it could be concluded that coordination phenomena are not exclusively rooted in purely reciprocal motor, especially neuromuscular-skeletal constraints (Oullier et al. 2005b).

Executed versus imagined uni- and bimanually opposition movements with maximal rate and accuracy were investigated by Nair et al. (2003). The supplementary motor area and the superior parietal cortex were activated during both imaging and physically performing the different self-generated sequential tasks, albeit to varying degrees. As cerebellar regions were hardly active in the imagery condition, it was stated that cortico-cerebellar loops may contribute primarily to actual movements by managing the cortical output through feedback corrective information to the motor cortex (Nair et al. 2003). Due to the accepted similarities in neural activity between real movements and imagined ones, in fMRI studies motor imagery is used to replace actual movements because the execution of especially gross-motor skills is not possible (Godde & Voelcker-Rehage 2007). An extended range of research could demonstrate that many of the same brain regions involved in real perception and action are also active in imagined perception and action (Marques & Holland 2009); shown during visual perception by Ganis et al. (2004) and Kosslyn et al. (1999); during motor action by Gerardin et al. (2000), Jahn et al. (2004), Papaxanthis et al. (2002) and Sahyoun et al. (2004); and even when an emotion is imagined, observed or executed (Jabbi et al. 2008). The partial overlapping neural networks for real and imagined movements lead to similar, but not identical brain activation. Differences were found at the final motor output stage as expected, which is not involved during motor imagery (Gerardin et al. 2000), and in the coupling between electrodes in the beta frequency range of electroencephalography (EEG) data (Kilner et al. 2004). Consequently, it is not surprising that at least a certain amount of the intrinsic dynamics is represented by central neural activity, and is, as a result, predefined without involve-