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Constraints on Coordination

Intrinsic dynamics, behavioral information and asymmetry in bimanual rhythmic coordination

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RIJKSUNIVERSITEIT GRONINGEN

Constraints on Coordination

Intrinsic dynamics, behavioral information and asymmetry in bimanual rhythmic coordination

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Martine Hendrika Geertruida Verheul

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General

Introduction

1.1 The Dynamic Systems Approach to Motor Coordination

Adequately coordinating movements in a constantly changing environment is a highly complex task, when one considers the many components involved. Yet, most of the time we coordinate the many parts of our body without thinking. When we do think about coordination, many questions arise. How do we integrate the nervous system, the sensory systems and the musculo-skeletal system? How are the limbs linked together in order to move in the coherent manner that they do? How is perception linked to the coordination of those limbs? How do intentions guide our movements, or, as Kelso (1994) states: "How does mind get into muscle?" A robot (or rather, a computer) has been shown to be better at chess than the human world champion, but no robots have been built yet that can move about in the world as effectively as we can (Keijzer, 1999). Apparently, the problem of coordination is solved by our body in such an efficient manner that we do not recognize the accomplishment until we try to imitate it or when our body fails.

The central concept in the classical approach to motor control, also called the information-processing approach, is the *motor program*. A motor program can be defined as an internal representation that prescribes the activity of the effector components underlying the movement (Schmidt & Fitzpatrick, 1996). There are several problems with a motor control theory based on the concept of a motor program. First of all, it hinders continuity between psychology and its related sciences, i.e., biology, physics and chemistry (Schmidt & Fitzpatrick, 1996; Schöner & Kelso, 1988b). There is no common language. The information processing approach regards motor control as rule-governed, rate-independent manipulation of symbol strings. This conception of control processes is far removed from the way the structure of the action system is conceived in the fields of for example functional anatomy, biochemistry and neuroscience. It is often unclear how a motor program relates to the characteristics of the motor system. The models do not address the question how the representational instructions are transformed into actual sensorimotor actions. Global instructions are handled by motor programs, but the representation-based architecture has great difficulty explaining how local instructions of numerous lower level parameters of the system can be coordinated (Keijzer, 1997).

Secondly, the nature and complexity of human functioning requires a far greater flexibility and adaptability than any theory of representational structure

has. In human functioning many unpredictable situations are encountered and have to be dealt with in an adaptive and functional manner. The representational structure therefore has to be constantly adapted to the constantly changing external world in order to be functional (Beek et al., 1995; Keijzer, 1997).

The third and most fundamental argument is the isomorphism between what needs to be explained and the explanation in a representational account of motor control (Schmidt & Fitzpatrick, 1996; Turvey & Carello, 1981). Knowledge of the required outcome of the manipulations has to be present in the mind (Keijzer, 1997). This requires an intelligent homonculus and is a replacement of the problem from outside the organism to inside the organism's head, or a *loan of intelligence* in the explanation of intelligence (Dennett, 1978). In other words, motor programs do not give insight into the underlying principles for their existence. There exists an enormous amount of seemingly unrelated models of processes and specific kinds of representations linked to the experimental paradigms used. Performance in any one task has been found to be multiply determined and the determinants seem to be task-specific. The approach is thus lacking in illuminating the bigger picture (Thelen & Smith, 1994).

This thesis is founded in an approach to motor coordination that starts from the idea that there is a circularly causal relationship between mind, brain and behavior (Kelso, 1998). Neither one of these is the proprietary level of explanation. It is in the interaction that control arises. This approach is called the *dynamic systems approach* to motor coordination. Instead of having mental prescriptions or representations for producing an action, knowing how to perform an action is regarded as relating to the laws of nature, so they can be used to create the required organization of the action system (Schmidt & Fitzpatrick, 1996). This does not deny that a structural correlate exists tantamount to a mental representation, but it takes issue with what that structural correlate is:

> "There is no doubt that structural changes occur within the actor when a skill is learned. The question is what these changes consist of. The claim of the dynamical perspective is that the structural changes should not be viewed as the addition of a prescription of action components (i.e., a list of what to do when, encoded in symbol strings), but an emergent set of relations between CNS, action system, and environmental properties that form a dynamical system and manifest the action as an aposteriori consequence. Hence, what we propose is that what is learned should be

understood as a set of physically encoded dynamical predilections of an action system rather than a motor program." (Schmidt & Fitzpatrick, 1996, p. 199).

The introduction of arbitrary representation of information is avoided by using a common language (synergetics, see paragraph 1.3) with which relevant information can be identified by its effect on the dynamics of behavior (Schöner, 1989). As will be shown below, psychological aspects such as attention and memory are captured in the same language as for example biomechanical and energetic aspects. The dynamic systems approach to motor coordination is closely linked to ecological psychology, the former being more concerned with the coordination between limbs or parts of limbs and the latter more with the coordination between perception and action (Turvey, 1990). Tools and concepts in the dynamic systems approach are borrowed from the sciences.

1.2 The problem of coordination: Redundancy of degrees of freedom

Nicolai Bernstein (1896-1966), in studying the hammer movement, observed that no two successive movements are exactly alike (Bernstein, 1967; Latash & Turvey, 1996). He theorized that, because external forces work on the movement apparatus and because the initial position of the limbs can vary greatly, a straightforward one to one relation between the nervous impulses and the motor behaviour cannot be expected. The many central and peripheral subsystems that compose the biological movement system will all contribute to the final motion. This is referred to as the *principle of functional non-univocality*. Bernstein defined coordination as the problem of mastering or reducing the many degrees of freedom (i.e., independent variables) involved in a particular movement, without ascribing this process entirely to some intelligent homunculus inside the nervous system. Bernstein suggested that movements are defined functionally by abstract or *topological* features, just like the letter *A*, for instance. It can appear in various sizes and shapes (e.g., very round or very angular), but it will, within certain boundaries, be perceived as an *A*. For an explanation of coordination, a general description of movements would be necessary, in which the many degrees of freedom are reduced to just a few. At that level, motor *control* is possible.

In line with Bernstein's ideas, Kugler et al. (1980) defined coordination as the function that constrains the potentially free variables into a behavioral unit. It is

the formation of *coordinative structures*. Coordinative structures are functional assemblies of muscles for a specific pattern of coordination. Kugler et al. purposefully put the emphasis on the role of constraints in coordination. Note that constraints are in fact the complementary parts of degrees of freedom. Constraints and degrees of freedom are defined by each other. For example, the anatomy of joints constrains movement. The elbow, for instance, can be regarded as a hinge-joint, with consequently only one degree of freedom, whereas the shoulder (a ball-joint) has more degree of freedoms. In more traditional theories constraints were always implicit or not addressed at all (Newell, 1986). In the approach of Kugler et al. (1980), constraints are central. They channel and guide the dynamics. Actions are not caused by constraints, but they are exluded by them. Constraints are permissive rather than deterministic. Newell (1986) developed a model of the categories of constraints on (the development of) coordination, that specify the optimal pattern of coordination and control. He subdivided constraints into environmental, task-related and organismic constraints. The borders between these categories are not clear-cut. For example, the room in which one does an experiment will often be an environmental constraint, but when it is explicitly manipulated it is a task constraint. Organismic constraints can be relatively time-independent such as body weight or relatively time-dependent such as motivation or attention. Task constraints are related to the goal of the task (i.e., outcome), the rules of the task that specify a specific coordination pattern and the implements or machines used in a task.

But how then does coordination come about within these constraints? To answer this question, modern movement scientists have turned towards the disciplines of physics and chemistry for help. Researchers within these disciplines had discovered that in complex open systems, i.e. systems comprised of multiple interacting elements in which there is an in- and outflow of energy, spatio-temporal patterns can arise spontaneously. These patterns are not prescribed anywhere in the microscopy of the system. Examples from the inanimate world are plentiful: the generation of laser-light (Haken, 1996), the Belousov-Zhabotinsky reaction: two chemical substances producing a clock-like alternation between two states (Aliev & Rovinsky, 1992; Welsh, 1984; Winfree, 1987), but also the more familiar phenomenon of circular patterns in a heated fluid (Haken, 1996). The same mechanism has been argued to account for the coordinated behaviour of groups of insects (e.g., Lewin, 1993). The premise of the dynamic systems approach to motor coordination is that motor coordination can be

regarded as a self-organizing property, guided by constraints. The constraints eliminate potential configurations of response dynamics. The resulting patterns show a self-organizing optimality: a continuous search for a stable pattern of coordination and control that accommodates the prevailing constraints (Kugler et al. 1980; Newell, 1986).

1.3 Coordination as a self-organizing property

Hermann Haken (1987; 1988; 1989; 1994; 1996) developed an interdisciplinary theory of self-organization, *synergetics*, based on observations of pattern-formation and sudden transitions between stable states in physical systems (non-linear dynamics). Synergetics is a theory about reduction of degrees of freedom, or *information compression*, in dynamical systems. A system is conceived of as a multi-layered complex process. Dynamic systems change over time. The neuro-motor system is pre-eminently a dynamic system and clearly generates spatio-temporal patterns. Therefore, synergetics was expected to be useful in describing coordination. Central in synergetics is the *slaving principle*, an essential prerequisite for information compression. Microscopic behaviour may be chaotically fluctuating, when an accidentally winning macroscopic behaviour will be strengthened by pulling the rest of the microscopy into this behaviour, generating a stable pattern at the macroscopic level. The microscopy generates the macroscopy, which in turn steers the microscopy. Because of this *circular causation* the system can self-organize into a stable state which can be described with only a few parameters. To describe the changes of the macroscopy over time, movement equations or potential equations are used.

Within the framework of synergetics, motor coordination is conceived as a spatiotemporal property emerging from a complex microscopy. The Haken-Kelso-Bunz model (*or:* HKB model; Haken et al., 1985) is a synergetic model of rhythmic interlimb coordination. This model considers moving limbs as coupled oscillators using the *relative phase* between the oscillators as the key variable to describe coordination. Rhythmic coordination is described in terms of the temporal stability (or variability) of the relative phase. It is based on experimental data of bimanual rhythmic finger tapping and finger and wrist abduction / adduction movements (Kelso, 1984; Kelso et al., 1986). Kelso and co-workers observed that when speed is increased in an anti-phase tapping task (moving the hands anti-symmetrically), a switch to an in-phase (synchronous) pattern is

frequently observed. When speed was subsequently decreased the system stayed in the symmetric phase relation. When the same study was done starting in an in-phase movement, no phase transition was observed. So, at low frequencies the system was observed to be bi-stable, while beyond a critical frequency only one coordination pattern could be performed in a stable fashion.

In the HKB model, the local minima of a potential function represent the coordination patterns that can be performed with temporal stability (Fig. 1.1). Those stable patterns are the in-phase pattern and the anti-phase pattern, with the in-phase pattern being more stable than the anti-phase pattern (lower minimum with steeper slopes). By increasing the movement frequency, represented by a so-called *control parameter* in the model, the anti-phase pattern can be shown to lose stability at a critical frequency. Several phenomena, such as increased variability and decreased perturbation resistance prior to a pattern-switch, are described with this model.
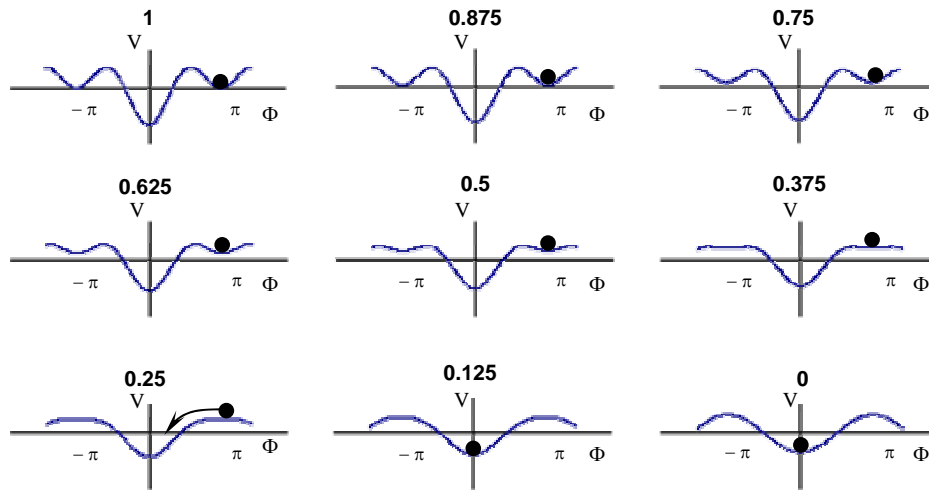
Figure 1.1. The potential landscape of the Haken-Kelso-Bunz model (Haken et al., 1985). When the control parameter has value 1 (upper left) the system is performing a stable anti-phase, or alternating, coordination pattern (π radials). When the control parameter is gradually scaled to 0, the anti-phase coordination pattern becomes unstable (the trough becomes shallower and eventually disappears) and a transition to in-phase coordination (0 radials) takes place.

The model has been used and expanded in a large number of follow-up studies on the effects of several constraints like handedness (Treffner & Turvey, 1995; 1996), biomechanical characteristics in the shape of asymmetrical eigenfrequencies (Fuchs et al., 1996; Jeka & Kelso, 1995; Peck & Turvey, 1997; Schmidt et al., 1991, 1993; Sternad et al., 1992; Treffner & Turvey, 1995; 1996), learning (Schöner, 1989; Zanone & Kelso, 1992; Walter & Swinnen, 1992) and intention (Scholz & Kelso, 1990; Schöner & Kelso, 1988a; Smethurst & Carson, 2001). The basic findings can be generalized to intra-limb multi-joint coordination such as between the elbow and wrist of the same arm (Kelso et al., 1991; Buchanan & Kelso, 1993), coordination between non-homologous limbs, i.e. arm and leg (Kelso & Jeka, 1992; Jeka & Kelso, 1995), and between all four limbs (Jeka et al., 1993). Even perception-based couplings display similar coordination dynamics, as evidenced by studies on inter-personal coordination of limbs (Amazeen et al., 1995; Schmidt et al., 1990, 1994, 1998; Schmidt & Turvey, 1994), and coordination of a finger, hand or lower arm with an external visual or auditory rhythmic signal (Byblow et al., 1995; Kelso et al., 1990; Wimmers et al., 1992). Note that variables of a very different nature are captured in the same language, and interactions between them can be investigated. This emphasizes the interdisciplinarity of the approach. Since the object of study is motor control, it involves the implicit integration of processes of a very different nature. Beek et al. (1995) proposed a model (Fig 1.2), in which three key entities for the organization of perceptual-motor actions are depicted, namely information, force, and matter.
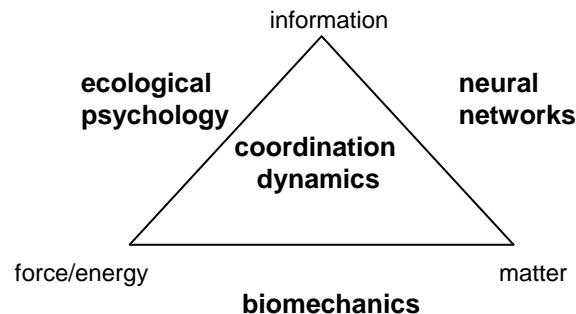
Figure 1.2. Tentative model depicting the relationship between coordination dynamics and related scientific research areas (Beek et al., 1995).

Traditional disciplines like psychology, mechanics, and anatomy deal with one of the three corners of the triangle. Contemporary approaches such as ecological psychology deal with the relationships between two entities. Coordination dynamics, however, is a more abstract approach and is concerned with phenomena arising from all the relationships in the model.

1.4 Aims and outline of the thesis: constraints on bimanual rhythmic coordination

It was argued above that constraints channel and guide the coordination dynamics. They set the conditions within which self-organization can take place. Constraints can be defined as the boundaries which limit the number of co-ordination states available to a dynamical system at any instance of its search for an optimal state of organization (Newell, 1986). They are thus essential prerequisites for the emergence of motor co-ordination. The emphasis the dynamic systems approach to motor control places on multi-causality has an important implication for research into motor control: the various elements together causing motor coordination should not be investigated in isolation. Newell stated:

> "A key point is the recognition that the optimal pattern of coordination is specified by the *interaction* of the three sources of constraints, namely, organismic, environmental and task." (Italics as in original text; Newell, 1986, p.354).

Although the constraints model was originally developed as a model for the emergence of coordination on a developmental time-scale, the model is often used as a general model of motor control. This thesis investigates the interaction between intrinsic (or organismic) and task constraints in the rhythmic coordination of two hands. The task that is studied is bimanual rhythmic tapping. This type of coordination is not as ecologically relevant as walking, talking or chewing. However, it is an easily accessible coordination task, which has been shown to reveal properties of motor coordination that are of general importance (e.g., Schöner & Kelso, 1988b; Kelso, 1998).

    Chapter 2 of this thesis focuses on the interaction between the intrinsic dynamics a person brings to the task and the behavioral information available

during task performance. Young adults with and without musical experience are compared when tapping more and less familiar coordination patterns (the in- and anti-phase and the gallop, i.e. a 90°-phase pattern). The patterns are offered in both an abstract manner and an ecologically relevant manner. Since the results revealed asymmetries in task performance that could not be fully understood in the present research design, the interaction between intrinsic asymmetry (hand-preference) and task asymmetry (the gallop) is further explored in *Chapter 3*. Left- and right-handers tapped the gallop pattern with their left hand and with their right hand leading, and the anti-phase pattern for comparison, under symmetric and asymmetric visual feedback conditions. In *Chapter 4*, the same experiment is repeated with Parkinson patients and a matched control group to investigate whether the coordination problems in Parkinson patients are a direct result of an inability to couple the limbs effectively, or whether they are (partly) the result of asymmetrical biomechanical changes of the limbs. In *Chapter 5*, findings are evaluated and discussed with an emphasis on their meaning within the framework of the dynamic approach to motor coordination. Also, the position of the dynamic approach in the wider field of motor control is addressed, from a philosophy of science perspective. Finally, future research directions are addressed.

2

Bimanual Coordination and Musical Experience

The role of intrinsic dynamics and behavioral information
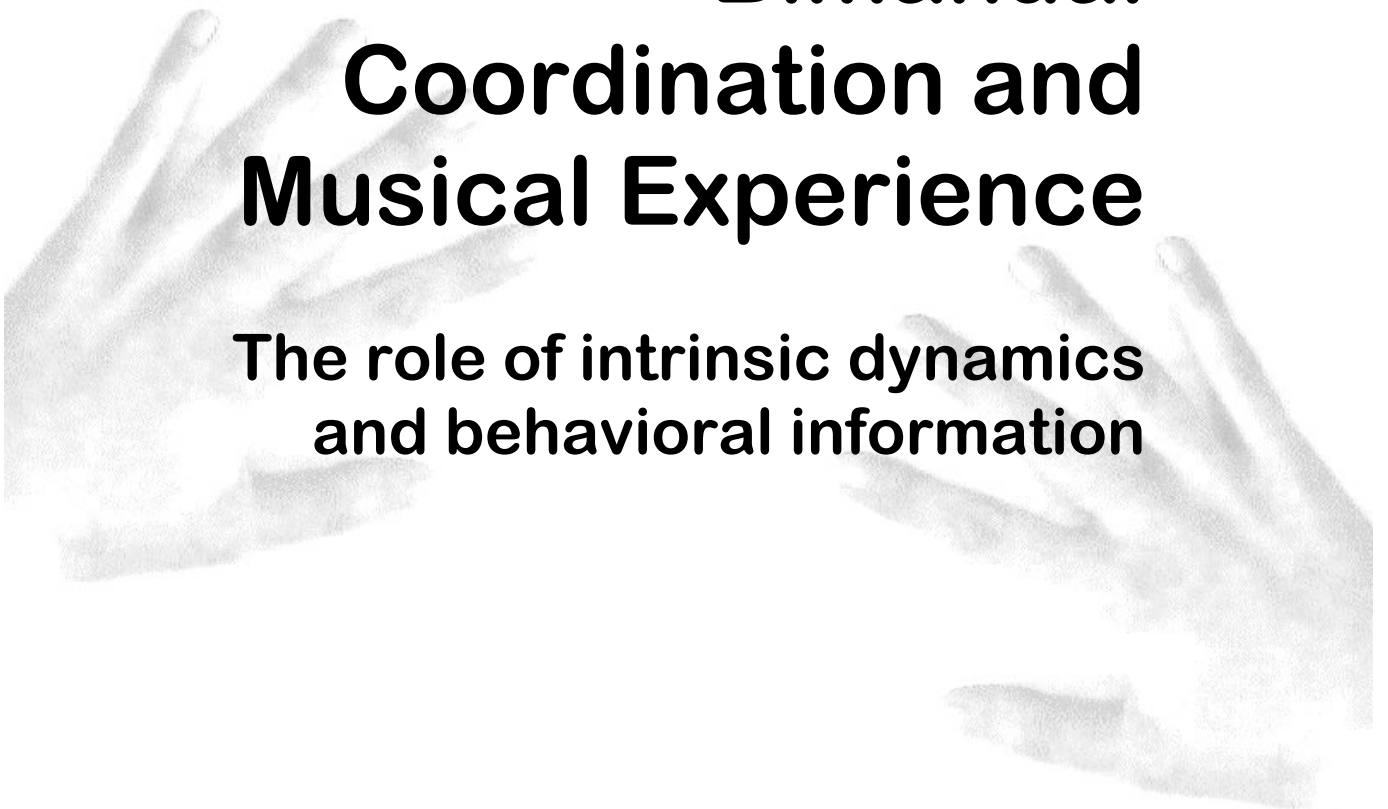
Abstract Rhythmic interlimb coordination arises from the interaction of intrinsic dynamics and behavioral information, i.e., intention, memory and/or external information specifying the required coordination pattern. This study investigates the influence of the content of memorized behavioral information on coordination in musically experienced and inexperienced subjects. These groups are hypothesized to have different intrinsic dynamics for this task. Stability was assessed in a switching task (variability and switching time). The in-phase, anti-phase and 90°-phase difference were specified in a neutral and an ecologically relevant manner. Musicians showed more stable coordination than non-musicians did. No interaction effect was found with memorized behavioral information. Behavioral information showed an interaction effect with phase pattern on coordination variability, with the strongest effect for the 90°-phase pattern. Switching time was affected largely in line with the findings for coordination variability. Subjects showed an intra-individual preference for one type of gallop and one type of switch strategy, suggesting different hand roles for the two hands.

2.1 Introduction

In the last two decades, the dynamic systems approach to interlimb coordination has focused on explaining systematic coordination tendencies in terms of a non-linear interaction of organismic, environmental and task constraints (see Kelso, 1998, for a review). No single element has causal primacy; together all elements constrain behavior in such a way that coordinated behavior emerges. A major aim of the dynamic systems approach is to show that although coordination may appear top-down controlled, it in fact emerges from the interaction of a number of factors. Under the influence of control parameters with a non-specific effect, such as movement frequency in bimanual rhythmic tapping, spontaneous coordination tendencies have been shown to emerge, the so-called *intrinsic dynamics* (Haken et al., 1985). The intention to perform a certain pattern can be conceptualized as a *specific* behavioral influence (Schöner & Kelso, 1988a), similar to environmental information specifying a pattern, and the memory of a learned pattern (Schöner & Kelso, 1988b). Intention, perception and memory of specific behavioral patterns have been grouped together in the concept of *behavioral information* (Kelso, 1994; Schöner & Kelso, 1988a; Schöner et al., 1992). Behavioral information may interact with the intrinsic dynamics in a cooperative or competitive way (Schöner & Kelso, 1988b). Together they generate the dynamics that are observed in real-time behavior. This study investigates the interaction of the two dynamics by studying performance of a rhythmical coordination task with the support of different types of behavioral information in musically trained and untrained adults.

The intrinsic coordination dynamics of bimanual rhythmic movements have been accurately described by the model of Haken et al. (1985) in the form of a potential function (see Fig. 1.1). The model contains a stable in-phase (simultaneous activation of homologous muscles) and anti-phase (simultaneous activation of non-homologous muscles) pattern, so-called attractor states in the potential landscape. The model describes how a decrease in a control parameter, representing an increase in movement frequency, leads to an annihilation of the anti-phase attractor. Applied to bimanual finger tapping, this means that increasing frequency while tapping in an alternating (i.e., anti-phase) fashion will lead to a spontaneous transition to simultaneous (i.e., in-phase) tapping at a critical frequency. Starting with in-phase tapping, such a transition does not occur

(Kelso, 1981, 1984). The strength of an attractor can be derived from the stability of a coordination pattern (Kelso et al., 1986; Scholz et al., 1987).

2.1.1 *Behavioral information*

Schöner & Kelso (1988a) suggested that intention can be considered behavioral information, similar to environmental information and memory. Scholz and Kelso (1990) have shown that the manipulation of intention can modify the pattern dynamics, even preventing the transition under some conditions. In their experiment, intentional switching from in-phase to anti-phase allowed for stable anti-phase coordination at frequencies at which the anti-phase is not naturally stable in the intrinsic dynamics. Switching intentionally from the anti-phase to the in-phase pattern strengthened the in-phase attractor in a similar way. However, the influence of the intrinsic dynamics on the resulting behavior remained present in spite of intentional modifications. Switching from the anti-phase pattern to the in-phase pattern was significantly faster than switching in the opposite direction, a finding that was later replicated by Carson et al. (1996) for pronation-supination movements. In addition, the differential stability between the two patterns remained present. These findings confirmed the model predictions of Schöner and Kelso (1988a). In their model, intrinsic dynamics and behavioral information are described in the same terms. The behavioral information is modeled as a second attractor layout that is added to the intrinsic dynamics as described by Haken et al. (1985). The resulting dynamics is dependent on both intrinsic dynamics and behavioral information. Further support for the modifying influence of intention comes from a study by Lee et al. (Lee et al., 1996), in which subjects increased frequency in an anti-phase pattern. Fewer transitions to another phase pattern occurred in conditions in which subjects were instructed to maintain the anti-phase pattern than in conditions in which subjects were told not to resist a transition, so-called "do not intervene" conditions. This finding was recently replicated by Smethurst and Carson (2003). Especially appealing, though anecdotal, evidence for the influence of intention comes from a study by Kelso et al. (1990), in which a subject interpreted a syncopation task (i.e., finger flexion in anti-phase with the signal, *off* the beat) as *extension* of the finger *on* the beat. This subject was the only one of the seven investigated who did not show a phase transition to flexion *on* the beat or to phase wandering when metronome frequency was slowly increased. Although this emphasizes the effect of task

definition on the coordination dynamics (Kelso, 1994), a study by Carson (1996) showed that redefining the task from flex-on-the-beat into extend-on-the-beat does not simply invert the original transition phenomenon. In the latter study, subjects frequently showed transitions to flex-on-the-beat, as well as phase wandering, when prepared in an extend-on-the-beat pattern. When prepared in a flex-on-the-beat pattern, this never occurred. Together, these studies show the importance of both informational and neuromusculoskeletal constraints on coordination dynamics.

In addition to intention, behavioral information can also be present in the form of environmental information or memory (Schöner & Kelso, 1988b). Visual or auditory pacing generates a temporally structured environment specifying a required coordination pattern. Tuller and Kelso (1989) had subjects tap a wide range of relative phases specified by a pacing light for each index finger. Yamanishi et al. (1980) trained subjects in tapping the various phase patterns with visual pacing, then withdrew pacing after the first ten cycles of each trial and had the subjects perform the task from memory. In the latter case, relative phasing was specified by memory. The relatively higher stability of the in-phase and anti-phase pattern compared with intermediate patterns was present in both studies. Tuller and Kelso, however, reported less variable coordination and smaller deviances from the required relative phase than Yamanishi et al. (1980). The different nature of behavioral information provided in these two studies (environmental specification versus memory) has been argued to be a plausible source of the quantitatively different outcomes (Tuller & Kelso, 1989).

In addition to the type of behavioral information (intentional, environmentally-specified, memorized), the *content* also has a moderating effect on the coordination dynamics. In a study by Thaut et al. (1997) finger tapping in synchronization with a metronome was compared with tapping with music. The synchronization error was significantly reduced with rhythmic cuing embedded in music at a few specific frequencies, and tapping variability (i.e., the coefficient of variation of tapping intervals) was significantly lower with music at the lower frequencies (1 Hz and lower). In another study, pendulum swinging with rhyme words has been shown to generate a stronger coupling than pendulum swinging with non-rhyme words (Shockley & Santana, 1999). These studies suggest that strengthening the rhythmical content of environmentally-specified behavioral information or adding ecologically meaningful features to it enhances the quality of coordination. For the case of memorized behavioral information, content also

seems to have an effect on coordination. Learning a new rhythmic pattern with visual or auditory pacing has been reported to have a differential effect on the performance in a consecutive memory-specified self-paced task. Audition was found to be beneficial over vision for stabilizing the memory-specified pattern (Zanone & Athènes, 1999). In the present study, the content of memorized information is manipulated in line with the studies of Thaut et al. (1997) and Shockley & Santana (1999). The required pattern is specified either by a memorized neutral instruction concerning the phasing of the hands or by a more "ecological" instruction involving memorized information on the gaits of a horse, walking, trotting or galloping. We compared the two types of memorized information, both specifying the required phase patterns in a cooperative manner, with respect to their effect on the coordination dynamics of bimanual finger tapping. The more ecologically valid behavioral information is expected to be stronger and consequently lead to more stable coordination.

2.1.2 *Intrinsic dynamics: musical training*

As argued earlier, the effect of behavioral information depends on the intrinsic dynamics. The latter, however, could differ among individuals. The intrinsic dynamics are shaped by neuromuscular and energetic constraints as well as personal experience (Thelen, 1995). In the process of development, through exploration in the environment, one is likely to have selected and strengthened certain efficient and functional coordination patterns. The intrinsic dynamics that an individual brings to a task therefore include a history of explicit and implicit learning that might be different for different people. Because experience in generating bimanual rhythmic patterns is obviously gained from playing a musical instrument, it is plausible to expect that musical experience will strengthen the intrinsic dynamics. Neuroanatomical and neurophysiological data support the link between musical experience and bimanual coordination (Ridding et al., 2000; Schlaug, 2001). Reports on the influence of musical experience on coordination dynamics are, however, contradictory. Yamanishi et al. (1980) found a significant difference in stability of coordination between a skilled group of piano students in a music college and an unskilled group. Tuller and Kelso (1989) failed to replicate this finding in their study with skilled subjects and subjects with little or no formal music training. In the present study, a group of subjects with musical experience was compared with a group of subjects without musical

experience. In the musically inexperienced subjects, coordination stability was expected to be lower than in the experienced subjects in all required phase patterns. Moreover, the gain of stability with the manipulation of memorized information was expected to be relatively larger in the former, intrinsically less stable group.

2.1.3 *Intrinsic dynamics: coordination pattern*

Studies on the effect of behavioral information, such as the Scholz and Kelso (1990) and Lee et al. (1996) experiments, are mainly focused on the two most stable coordination patterns, the in-phase pattern and the anti-phase pattern. It could be expected, however, that relatively unknown and unstable patterns such as the 90°-phase pattern are more strongly influenced by behavioral information than the in-phase and anti-phase patterns are. The 90°-phase pattern appears to be a relatively weak attractor in bimanual finger tapping. In the experiments by Tuller and Kelso (1989) and Yamanishi et al. (1980), in which a wide range of phases was investigated, the in-phase and anti-phase patterns were shown to be significantly more stable than the intermediate phase patterns. Greater stability was found, however, around 0.25 and 0.75 than at other intermediate relative phase values in some subjects in both studies. Whitall (1989) also reported an asymmetrical phasing relationship between in-phase and anti-phase to be a stable pattern in children's running. Based on the observation by Whitall (1989), Peck and Turvey (1997) instructed subjects to swing a set of pendulums in a pattern that they were likely to have produced as a child when mimicking riding a horse. The dynamics accompanying changes in speed and eigenfrequencies of the 90°-phase pattern were qualitatively similar to those of the in- and anti-phase patterns and an extended Haken-Kelso-Bunz model (Haken et al., 1985) was suggested with two additional Fourier series terms to account for the bipedal galloping pattern. This model containing a weak 90°-phase attractor seems valid for the tapping task used in the present study, because it has been shown that tapping a 90°-phase pattern is stable without extensive practice (Verheul & Geuze, 2003). It has been argued above that all coordination patterns are likely to be more stable in musicians than in non-musicians. Thus, the hypothesized large effect of behavioral information on the 90°-phase pattern is expected to be particularly pronounced in the non-musicians.

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Coordination dynamics are assessed by stability and accuracy measures. In a continuation/switch task, coordination stability is measured in two distinct ways. In addition to determining relative phase variability during constant tapping, we assessed the time it takes to switch between patterns. Switching from an intrinsically more stable to an intrinsically less stable pattern has been found to take longer than switching in the reverse direction (e.g., Scholz & Kelso, 1990; Schöner & Kelso, 1988a). Although switch tasks have mainly been used in studies of the in-phase and anti-phase patterns, it is plausible that results can be generalized to the 90°-phase pattern. The expected effects of phase pattern on phase variability can therefore be rephrased in effects of switch condition (e.g., in-phase to anti-phase) on switching time.

A consequence of the switch task is that it provides two time series per trial for which coordination variability and accuracy can be determined: the pre- and post-switch time series. The two time series only differ with respect to what preceded them. Before the switch, subjects initiated tapping with a brief period of pacing (which was not analyzed) and continued without pacing, whereas after the switch the pattern had to be generated from memory from the onset. Therefore, coordination was expected to be more accurate before the switch than after the switch. No specific hypothesis was formulated with regard to coordination stability. Any effect of pre/post-switch origin of the data might be interpreted as an effect of the difference in behavioral information offered directly preceding the actual task.

Subjects were free to adopt different strategies when switching from one pattern to another (e.g., the hand that adapts its interval to acquire the post-switch phase pattern). They were also free to choose a left- or a right-leading 90°-phase pattern. Because the behavior of the subjects might be informative of systematic asymmetries underlying coordination, an exploratory analysis was focused on the presence of such systematic asymmetries. The model by Haken et al. (1985) assumes that the two hands are symmetrical, but some studies have suggested small but systematic effects of lateralization or handedness in symmetric bimanual coordination tasks (Stucchi & Viviani, 1993; Swinnen et al., 1996; Treffner & Turvey, 1996) and larger effects in asymmetrical (multifrequency) bimanual coordination tasks (e.g., Peters, 1994; Summers & Kennedy, 1992). The present study could show further signs of an asymmetrical control, supporting these studies.

2.2 Methods

2.2.1 *Subjects*

Twenty individuals participated (age 19-31, 10 women, 10 men). Half reported having no experience playing a musical instrument and were assigned to the non-musical group. The other subjects, with 0.5 to 9 years of experience playing a wind instrument, guitar, piano or keyboard, were assigned to the musical group. Two subjects reported being left-handed. Both had musical experience. This small proportion of left-handers (10%) mirrors the distribution in the general population (van Strien, 1992). The remaining subjects reported being right-handed. All subjects gave their written informed consent before the experiment. One right-handed non-musical female subject was unable to produce a stable 90°-phase pattern throughout the experiment and was excluded from the analysis.

2.2.2 *Apparatus*

Two touch-sensitive buttons (diameter 2.5 cm, 7.5 cm apart), built in the slanted surface of a box (30 x 20 x 2 to 6 cm), registered finger taps with an accuracy of 1 ms. The taps produced a slight sound when the buttons were touched. The box also served as a support for the hands. A personal computer generated auditory pacing signals (neutral "click" sounds or recorded hoof-beat sounds, duration 75 ms) for both hands at the beginning of each trial, specifying either a 0°, 90° or 180° phasing between the hands. In the center top of the box, a red light-emitting diode (diameter 3 mm) signaled the switch. During pacing in the neutral condition a static picture of a subject performing the tapping task was presented to the subject on a monitor. In the horse analogy condition, animations consisting of eight frames were presented on the same monitor (Fig. 2.1). The hoof-beat sounds were coupled to one or two animation frames in which the front legs of the horse hit the ground, generating a walk (one leg), trot or gallop (two legs) pacing.

walk
(in-phase)

trot
(anti-phase)

gallop
(90°-phase)
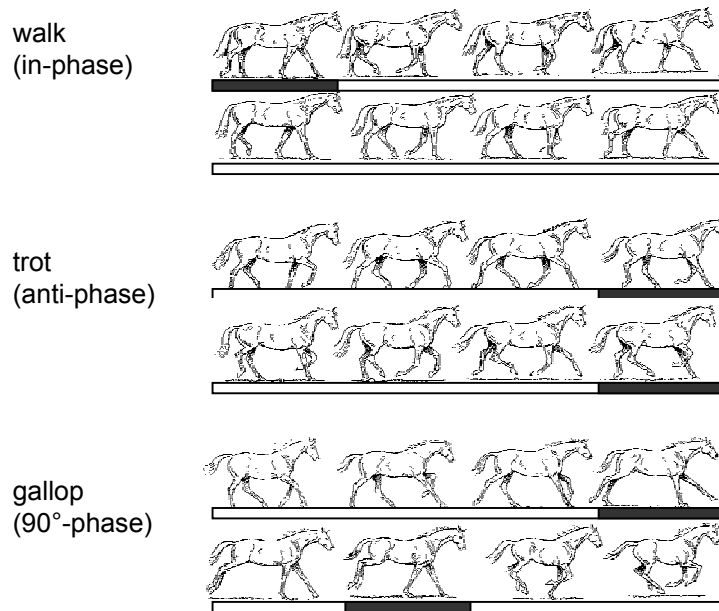
Figure 2.1 Animation shown to the subjects at the beginning of each memorized horse gait trial. Frame rate of the horse gait animation was 100 ms. Black bars indicate the timing of the hoof-beat sounds, pacing each finger at 1.25 Hz.

2.2.3 *Procedure*

Subjects were seated comfortably at a table facing the monitor. Their hands rested on the box, and their index fingers on the two buttons. Subjects were asked to tap with their index fingers on the buttons in a continuation/switch task. They were instructed to tap as constantly as possible in one of three phase patterns (in-phase, anti-phase or 90°-phase difference) at an initially paced frequency (1.25 Hz for 6 cycles, i.e., 4.8 seconds), and to continue tapping after the pacing had stopped. At two-thirds of the trial, 19 tapping cycles after pacing, a light was presented coincident with a left finger tap, to indicate that the subjects were to switch to another, pre-specified pattern. The instruction was to switch promptly to the other

pattern. After switching, subjects continued tapping, until signaled by the experimenter to stop. This resulted in approximately 15 seconds of self-paced tapping before the switch, and approximately 10 seconds (13 recorded left finger taps) after the switch. Each switch trial lasted approximately 30 seconds, including the paced period.

The three patterns were first tapped under a "neutral" instruction set, and then in the "memorized horse gait" condition. Because of the nature of the manipulation, order was necessarily fixed. In the neutral behavioral information condition, subjects were instructed to tap with their fingers simultaneously (in-phase), alternating (anti-phase), or in an unequal manner (90°-phase difference). In the memorized horse gait condition, subjects were instructed to imagine their fingers being the front legs of a trotting (anti-phase) or galloping (90°-phase difference) horse. In the 90°-phase condition, subjects were free to perform the pattern with either their left hand leading or their right hand leading. During the pacing period of the walk (in-phase) condition, both fingers were to tap simultaneously with the displacement of a single leg of the horse. The horse animation and hoof-beat sounds were intended to help subjects memorize the horse gait patterns before the self-paced tapping in the remainder of the trial. Horse gaits were chosen, because they are familiar, naturally occurring patterns.

All six possible switches between the three phase patterns were performed first three times with initial neutral pacing and then three times with initial hoof-beat pacing and related animations, making a total of 36 trials. The trials were organized in 6 blocks, each consisting of the six switch conditions in random order. The first three blocks (i.e., 18 trials) were performed under the neutral instruction set, and the remaining three blocks with the ecological "horse gait" instructions. Practice trials of three randomly chosen switches were given with the limitation that each phase pattern was tapped once before and once after the switch.

2.2.4 *Data reduction*

Only the self-paced parts of the trials were analyzed. The parameter describing coordination is the relative phase (ϕ), calculated as follows:

$$\phi = (L_n - R_n)/(R_{n+1} - R_n) \times 360° \tag{1}$$

in which *L* and *R* are the points in time at which the left and right index finger hit a button. In the 90°-phase condition, the leading hand interval was taken as the denominator in the calculation of the relative phase. This had no consequences for the calculation of the relative phase in a right-leading 90°-phase pattern, but in the case of a left-leading 90°-phase pattern the relative phase was calculated as

$$\phi = (R_n - L_n)/(L_{n+1} - L_n) \times 360° \qquad (2)$$

Note that through this calculation both the left- and right-leading pattern are indicated by a relative phase of 90°. This method was chosen because the intertap intervals of the leading hand in a galloping task are more stable than the intertap intervals of the non-leading hand (Verheul & Geuze, 2003).

Coordination stability was assessed by calculating the variability (i.e., standard deviation) of the relative phase during constant tapping and the switching time. The variability of the relative phase was calculated both for pre- and post-switch non-paced stable tapping. Thus, per individual the 36 trials generated 72 time-series: 36 pre-switch and 36 post-switch. Switching time was calculated as the time between the onset of the switching signal and the initiation of the post-switch pattern (i.e., the first tap after the switching signal that makes up the required phase pattern ±45° with consecutive taps). Because frequency differed slightly between trials at the moment the switching signal was presented, relative switching time was calculated as the percentage of pre-switch cycle duration (Geuze, 2001). Accuracy was assessed by calculating the absolute error for each pre-switch and post-switch part of each trial (i.e., absolute deviation from the required relative phase).

Furthermore, switching strategies were assessed by visual inspection. Strategies were characterized by the speeding up or slowing down in one or more post-switch intervals of a single hand or both hands in order to change the coordination pattern. This resulted in six possible strategies: right faster (RF), left faster (LF), right slower (RS), left slower (LS), right faster and left slower (RFLS) and right slower and left faster (RSLF). For each subject, one or two dominant switching strategies per switch condition were determined if present (i.e., a strategy adopted in 3 or more trials out of the 6 trials in that switch condition). Strategies were also combined on the basis of their common effect on the coordination level into a right faster and/or left slower (RF, LS, RFLS) and right slower and/or left faster (RS, LF, RSLF) strategy.

2.2.5 *Statistical analysis*

A multilevel random slope model for repeated measures was used for statistical analysis (Appendix IV). This type of regression model differs from the usual multiple regression in the fact that the equation defining the model contains more than one error term: at least one for each level. This makes this type of model suitable for data from repeated measures (level 1) in multiple subjects (level 2). The multilevel model describes a collection of multiple regression models (one for each subject) with varying intercepts and slopes. Since we presented the neutral and horse gait conditions necessarily in fixed order, we needed to test the effect of the gait analogy *given* a possible learning effect on the coordination measures. With the multilevel regression model we were able to test for a significant change in the value of the dependent variable between the third and fourth blocks of trials *in addition to* a change from the first to the sixth block that resulted from learning. We also tested the effects of musical experience, phase pattern, pre/post-switch (the latter two not for switching time) and switch condition (only for switching time), and all 2- and 3-way interactions. *T*-tests and deviance tests (Chi-square) were used to evaluate the improvement of the model fit by inclusion of an effect. "Post hoc" results for main effects with more than two levels and for 3 x 2 interaction effects were derived from dummy variables. Because of the large number of degrees of freedom with tests involving lower-level variables (all except musical experience), *t*-values were treated as standardized *z*-scores where applicable. Deviance tests were used for multi-parameter testing, such as multiple pair-wise comparisons. The significance level α was set at .05.

2.3 Results

2.3.1 *Intrinsic dynamics*

Consistent with our hypothesis, coordination was significantly more stable in the subjects with musical experience than in those without, according to both stability measures (Table 2.1). First, musicians showed lower relative phase variability than did non-musicians ($t(18)$= -2.84, $p<.01$). Second, musicians switched significantly faster than non-musicians did (absolute switching times $t(18)$ = -

3.46, $p<.01$; relative switching times $t(18)= -3.31$, $p<.01$). Average relative switching time per subject ranged from 74% to 152% of the pre-switch cycle duration. In addition to the effects for coordination stability, musicians were significantly more accurate than non-musicians as evidenced by a significantly lower absolute error (Table 2.1, $t(18)=-2.34$, $p<.05$).

Table 2.1 Main effects of musical experience.

	No musical experience	Musical experience
Relative phase variability (°)	9.7 (1.7)	7.8 (1.4)**
Switching time (ms)	913 (122)	735 (109)**
Switching time (%)	122 (19)	98 (14)**
Absolute error (°)	8.8 (3.7)	7.7 (3.1)*

Note. Group means. Between-subject variability (standard deviation) between brackets. *p<.05, **p<.01.

The most pronounced effects were those of phase pattern (Table 2.2). Relative phase variability differed significantly between phase patterns as expected ($\chi^2(2)=397.3$, $p<.001$). The in-phase pattern showed the lowest variability, and the 90°-phase pattern the highest. Pair-wise comparisons showed that each phase pattern differed significantly from both other patterns (all $p<.001$). Phase pattern also had a highly significant effect on accuracy ($\chi^2(2)=750.9$, $p<.001$). The absolute errors in in-phase and anti-phase did not differ significantly, but accuracy was significantly more compromised in the 90°-phase pattern than in the in-phase and anti-phase patterns (pair-wise comparisons both $p<.001$). In contrast to the effect of phase pattern for relative phase variability, switch condition (e.g., in-phase to anti-phase, anti-phase to 90°-phase pattern, etc.) had no significant main effect on switching time. The average switching time was 818 ms, or 109 % of pre-switch cycle duration.

The interaction between musical experience and phase pattern was not significant for relative phase variability or for accuracy. In addition, no significant interaction between musical experience and switch condition was found for switching time. Subjects with musical experience showed more stable and more

accurate coordination in all phase patterns and switched faster in all switch conditions than did the subjects without musical experience. The difference in relative phase variability between the two groups was largest (2.4°) in the 90°-phase pattern, whereas the difference in accuracy was largest (1.9°) in the in-phase pattern. The largest difference in switching time (32%) was found for the switch from the 90°-phase pattern to in-phase.

Table 2.2 Main effects of phase pattern.

	In-phase	Anti-phase	90°-phase
Relative phase variability (°)	6.8_a (1.7)	8.0_b (1.9)	11.3_c (3.2)
Absolute error (°)	3.6_a (2.2)	4.1_a (1.5)	17.2_b (9.1)

Note. Mean performance in each phase pattern. Between-subject variability (standard deviation) between brackets. Means with different subscripts differ significantly at p<.001.

2.3.2 *Behavioral information*

Contrary to our expectation, no main effects of the manipulation of behavioral information (the gait analogy) were found for the coordination stability measures (relative phase variability and switching time) or for accuracy.

2.3.3 *Pre/post-switch*

No main effect of the pre- or post-switch origin of the data was found for relative phase variability. Pre-switch accuracy was however significantly higher than post-switch accuracy (z=4.46, p<.001). Pre-switch, the absolute error was 7.6°, rising to 9.0° post-switch.

2.3.4 *Interactions between intrinsic dynamics and behavioral information*

The central aim of this study is to assess the interaction between intrinsic dynamics and behavioral information. We hypothesized the manipulation of behavioral information (the gait analogy) to have a particularly strong effect on

non-musicians and in intrinsically less stable patterns, such as the 90°-phase pattern.

In contrast to our expectations, no significant interaction was found between group (i.e., musical experience) and the manipulation of behavioral information (the gait analogy) for any of the dependent variables. As expected, however, the manipulation of behavioral information showed a significant interaction effect with phase pattern for relative phase variability (Fig. 2.2, $\chi^2(2) = 7.76$, $p<.05$) and with switch condition for absolute and relative switching time (Fig. 2.3, $\chi^2(5) = 13.32$, $p<.05$; $\chi^2(5) = 13.96$, $p<.05$ respectively).
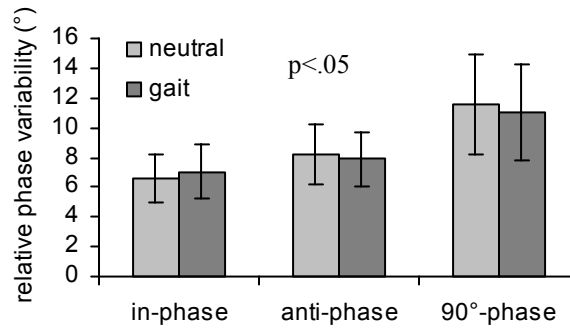
Figure 2.2 Relative phase variability of the three phase patterns in the neutral condition and in the condition with behavioral information in the shape of memorized horse gaits. Error bars indicate between-subject variability (standard deviation). Behavioral information had a significantly different effect on the in-phase pattern than the other patterns.

As expected, the gait analogy caused the strongest reduction of relative phase variability in the 90°-phase pattern. However, the significant interaction effect resulted from the gait analogy having a significantly different effect on the in-phase pattern than on the anti-phase and 90°-phase patterns ($p<.05$ and $p<.01$, respectively). In the in-phase pattern, the memorized gait condition was associated with an *increase* in variability rather than the expected decrease, whereas in both the anti-phase and 90°-phase patterns the gait analogy caused a decrease in variability (Fig. 2.2). The effect was not significantly different for the anti-phase and 90°-phase patterns.
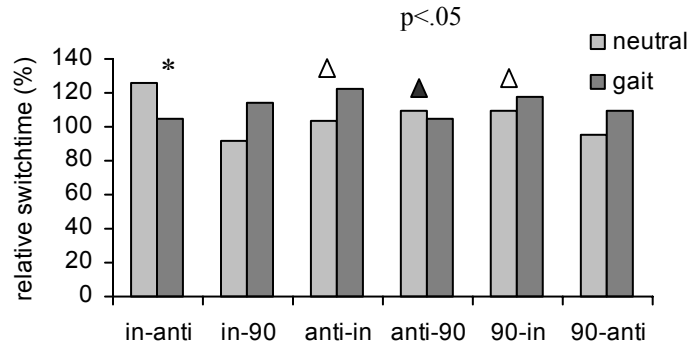
Figure 2.3 Relative switching time for each switch condition in the neutral condition and in the condition with behavioral information in the shape of memorized horse gaits. "In-anti" refers to the switch from in-phase to anti-phase, "in-90" refers to the switch from in-phase to the 90°-phase pattern, and so on. Behavioral information had a significantly different effect on the switch from in-phase to anti-phase (*) than all other switches, except for anti-phase to 90°-phase (black triangle), which differed significantly from the switches indicated by the white triangle. All effects at least *p<.05*.

Analysis of switching time was expected to generate results in line with the findings for relative phase variability. When relative phase variability is low (i.e., the pattern is stable), it would take relatively long to switch *from* that pattern, but a switch *to* that pattern would be performed relatively quickly. For a phase pattern with high variability, the reverse was expected. Because the largest stabilizing effect of the gait analogy was expected (and found) in the 90°-phase pattern, switches *to* the 90°-phase pattern would be expected to be faster and switches *from* that pattern slower in the gait condition than in the neutral condition. This was found to be the case, except for the switch from in-phase to the 90°-phase pattern. The destabilizing effect of the gait analogy we found for the in-phase pattern would translate into faster switching *from* the in-phase pattern and slower *to* that pattern. Again, this was the result we found, except for the switch from in-phase to the 90°-phase pattern. Combining these results, we expected the memorized gait to shorten switching times for the switch conditions in-phase to anti-phase, in-phase to 90°, and anti-phase to 90°, and to lengthen switching times for anti-phase to in-phase, 90° to in-phase and 90° to anti-phase. For all switch conditions except the in-phase to 90°, the results were in line with findings from the variability data (Fig. 2.3).

Post hoc analysis showed that the behavioral information had a significantly different influence on the in-phase to anti-phase pattern than on all other switches except for the switch from anti-phase to the 90°-phase pattern ($p<.05$ to $p<.001$ for individual comparisons). The effect that behavioral information had on the switch from anti-phase to the 90°-phase pattern differed significantly only from the effect on the 90°-phase pattern to in-phase switch for absolute switching time ($p<.05$), and from the latter and the switch from anti-phase to in-phase for the relative switching time. There was no significant effect of order on switching time or relative phase variability, suggesting that the revealed interaction effects can be attributed to the manipulation of behavioral information. The manipulation of behavioral information showed no significant interaction effect with phase pattern for accuracy.

2.3.5 *Interactions between intrinsic dynamics and pre/post-switch*

In addition to the behavioral information during the task, the *preceding* behavioral information also had a significant influence on performance in interaction with the intrinsic dynamics, as revealed by interaction effects of pre/post-switch with both musical experience and phase pattern. The difference in relative phase variability and accuracy between the two groups was significantly larger before the switch than after the switch (interaction effect for variability $z=2.39$, $p<.01$; interaction effect for accuracy $z = 2.65$, $p<.01$). This was the result of a combined increase in variability for the musicians and a (small) decrease in variability in non-musicians (Fig. 2.4), as well as a very accurate performance of the musicians before the switch (Fig. 2.5).
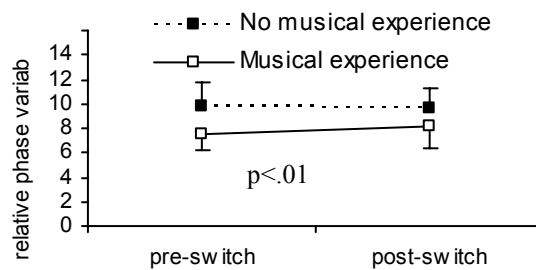
Figure 2.4 Relative phase variability before and after the switch for both groups. Error bars indicate between-subject variability (standard deviation).
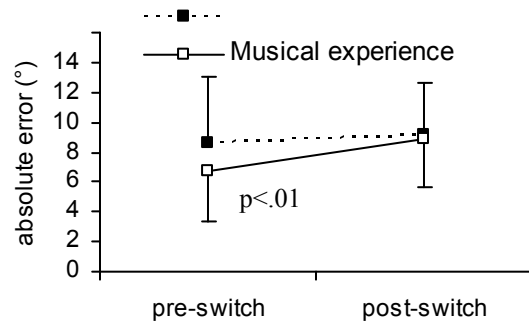
Figure 2.5 Absolute error before and after the switch for both groups. Error bars indicate between-subject variability (standard deviation).

Significant interaction effects were also found between phase pattern and pre/post-switch for both relative phase variability ($\chi^2(2)$=30.87, p<.001) and accuracy ($\chi^2(2)$=39.32, p<.001). For the in-phase and anti-phase patterns, variability was slightly lower after the switch than before the switch, whereas variability of the 90°-phase pattern was higher after the switch (Fig. 2.6).
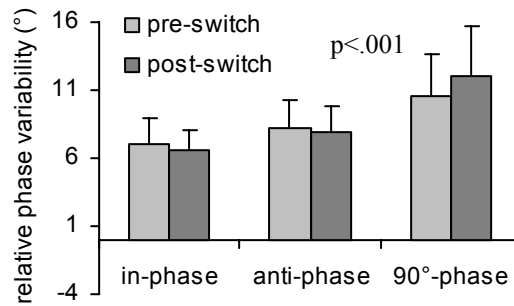
Figure 2.6 Relative phase variability before and after the switch for the three phase patterns. Error bars indicate between-subject variability (standard deviation). Pre/post-switch had a significantly different effect on the 90°-phase pattern than the other patterns.

Post hoc analysis showed that the pre- or post-switch origin of the data had a significantly different effect on the 90°-phase pattern than on the in-phase and anti-phase patterns (both *p*<.001). The absolute error in the 90°-phase pattern was

also significantly larger after the switch than before (Fig. 2.7). In the in-phase and anti-phase patterns, the error was similar before and after the switch. Again, post hoc analysis showed that the pre- or post-switch origin of the data had a significantly different effect on the gallop than on the in-phase and anti-phase patterns (both $p<.001$).
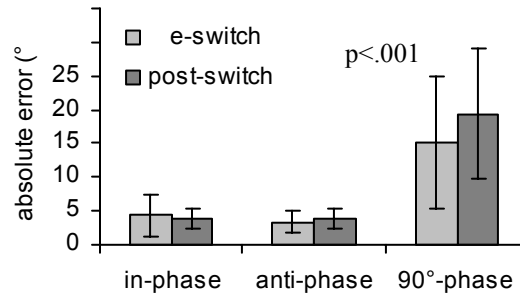
Figure 2.7 Absolute error before and after the switch for the three phase patterns. Error bars indicate between-subject variability (standard deviation). Pre/post-switch had a significantly different effect on the 90°-phase pattern than the other patterns.

The three-way interactions between group, pattern, behavioral information and pre/post-switch were not significant for relative phase variability and accuracy, and the three-way interaction group x switch condition x behavioral information was not significant for switching time.

2.3.6 *Choice of gallop and switch strategy*

Subjects were free to choose between a left and right leading gallop, but after the switch they might have been forced into their non-preferred type of gallop, because the switch signal was always presented coinciding with a left finger tap. Looking only at the choice of gallop before the switch, subjects adopted a right leading gallop in 73.4% of the successful 90°-phase trials. A high within-subject consistency was found. Four subjects chose a left leading gallop in at least 10 out of 12 trials. One of these subjects was left-handed. Twelve subjects showed a right-leading pattern in at least 11 out of 12 trials, with nine of them choosing this

pattern in all of the trials. One of these nine was left-handed. The remaining three subjects chose twice as often a right-gallop (8 times) than a left-gallop (4 times).

In order to switch, subjects had to adjust the timing of one or both hands. They showed a highly consistent switch strategy within each switch condition. For 13 subjects, one or two dominant strategies could be determined for each switch condition (see Methods). For the other 6 subjects, this could be done for at least 4 of the 6 switch conditions. Slowing down the left hand in order to change the coordination pattern was the strategy adopted most often. It was used more than twice as often as either one of the other strategies. In contrast to the intra-individual consistency *within* a particular switch condition, subjects were not consistent over different switch conditions. Looking at the effect on the level of coordination, their choice of strategy was systematic nevertheless. Subjects could be divided into two distinct groups. A majority of the subjects (n=15) adopted the strategy of slowing down the left hand, speeding up the right hand, or a combined strategy of slowing down the left and speeding up the right as their dominant strategy in 90% of all cases (switch conditions over all subjects), except the 90° to in-phase switch condition, in which an opposite strategy was used by all of these subjects. Four subjects showed the opposite strategies in all conditions. They speeded up the left hand, slowed down the right, or showed a combination of these in 88% of all cases, except the 90° to in-phase switch condition, in which all four used an opposite strategy. These were the four subjects who consistently adopted a left-leading gallop.

2.4 Discussion

The intrinsic dynamics of subjects with musical experience were characterized by stronger attractors than the intrinsic dynamics of the non-musicians. A significant group difference was found for relative phase variability and switching time, two measures of coordination stability. This finding is strengthened by the fact that the subject that had to be excluded from the analysis, because of an inability to tap the 90° pattern, was a non-musician. These data are consistent with the results of the study of Yamanishi et al. (1980), who found a significant difference in stability of coordination in a continuation task between a skilled group of piano students in a music college and an unskilled group. Tuller and Kelso (1989), however, found no difference in coordination stability between musically trained subjects (i.e., having played the piano, or piano and violin, for a minimum of ten

years) and subjects with little or no formal music training. Differences in behavioral information during the task could have accounted for this. In the Tuller and Kelso experiment the required pattern was environmentally specified by visual pacing throughout the experiment, whereas in the present experiment, as well as in the experiment by Yamanishi et al., the pattern was specified by memory. Musically skilled individuals might be superior in using memorized behavioral information for their control of coordination. It must be noted that this advantage appears to depend on the preceding events. In the present experiment, the difference between the two groups was found to be especially large before the switch, suggesting that the pacing preceding the pre-switch tapping could have had a particularly beneficial effect on the musical group. The musically experienced subjects were also more accurate than the non-experienced group, again especially before the switch. Apparently, the behavioral information is memorized better in musicians, but in an unstable manner, so that the advantage quickly diminishes by intervening events. Future research might differentiate between individuals with experience in musical settings that are dominated by environmental pacing, such as a band or choir, and subjects with experience mainly in generating self-paced music from tablature and sheet music. In addition, the influence of the type of musical instrument played (Christman, 1993) and the level of experience deserve further investigation.

The nature of memorized behavioral information did not affect coordination stability differently in musicians and non-musicians in the present study. The more ecological behavioral information stabilized the anti-phase and 90°-phase patterns, but decreased stability of the in-phase pattern, compared with neutral behavioral information, as measured by relative phase variability. Because no effect of order on relative phase variability was found, the data suggest that this interaction between behavioral information condition and phase pattern is caused by the informational content rather than learning. Results suggest that the horse gait analogy supplied cooperative behavioral information in the anti-phase (trot) and 90°-phase (gallop) conditions, but competitive information in the case of the in-phase (walk) condition. Since the correspondence between "walk" and the in-phase pattern was weak (see Methods), drawing attention to the horse gait may have lead to a double task situation in the in-phase condition. This could have decreased coordination stability, as supported by double task studies involving similar bimanual coordination tasks (e.g., Monno et al. 2000, 2002; Temprado et al. 1999; Zanone et al., 2001). In contrast, in the anti-phase and 90°-phase pattern,

the horse gait analogy may have supported the specification of the required coordination pattern.

These findings were largely supported by the effect of memorized gait on the other measure of stability (i.e., switching time). Extrapolating from the findings for relative phase variability, one would expect that switches from the in-phase in the memorized gait condition were faster than in the neutral condition, whereas switches to in-phase would be expected to take longer in the memorized gait condition. Conversely, switches from the anti-phase and the 90°-phase patterns would take longer in the memorized gait condition, whereas switches to these patterns would be faster in that condition. Results for five out of the six switch conditions confirmed these expectations. Only the switch from in-phase to the 90°-phase pattern showed the opposite result. The effect of the gait analogy on the switch could have been complicated by the fact that subjects tried not only to imagine the first pattern, and then the second, but also to imagine the transition in terms of a horse gait transition, which makes the transitions between in-phase and the 90°-phase pattern (walk and gallop, in both directions) particularly unnatural. It is apparent that manipulating the content of behavioral information requires further study. The few studies directed at the ecological content of behavioral information (Shockley & Santana, 1999; Thaut et al., 1997) suggest, along with the present study, that enhancing the cognitive meaning of the pacing signal may have a beneficial effect on coordination in specific task conditions.

The way the horse gait analogy was offered in this study may not have been the most effective way to change *memorized* behavioral information in the expected direction. The study of Zanone and Athènes (1999) could be relevant in this respect. This study suggests that auditory specification of a rhythmic pattern is beneficial over visual specification for the performance in a subsequent memory-specified self-paced task. In the present experiment, the horse gait analogy relied on visual specification to a larger extent than the neutral condition. In the neutral condition, the sounds specified the required pattern (a static picture was presented), whereas in the gait analogy condition, an animation was added to the hoof-beat sounds to aid memorization as much as possible. Taking Zanone and Athènes' study into account, this may have had a negative effect on consecutive memory-specified self-paced tapping.

Furthermore, the rhythmic contact of the fingers with the buttons provided "hard" landmarks and auditory and haptic feedback. Therefore, finger tapping might not be sensitive to the manipulation of cognitive constraints in the way that

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rhythmically coordinated movements that don't benefit from such rhythmic contact seem to be, such as supination-pronation movements of the forearms (Temprado et al., 1999), abduction-adduction movements of the hands (Amazeen et al., 1997) or the index fingers (Scholz & Kelso, 1990), and bimanual circle drawing movements (Wuyts et al., 1996). In these studies, the manipulation of focused attention changed coordination dynamics, including stability features. A recent study on bimanual 1:3 tapping showed no significant effect of the manipulation of the cognitive description of the task (Semjen & Vos, 2002).

The 90° or galloping pattern was performed with the lowest stability and accuracy. It differed from the other patterns especially with respect to accuracy. After initial pacing, subjects had difficulty maintaining the 90°-phase pattern, and shifted to values between 60° and 120°, maintaining stability at that shifted pattern. This suggests the 90°-phase pattern may *not* be a basic pattern, comparable to the in- and anti-phase pattern, only with lower stability. In our experiment one subject was unable to perform a stable gallop throughout the experiment. In a similar tapping task, Tuller and Kelso (1989) also found the gallop to be an attractor in some non-musicians, but not all. Peck and Turvey (1997) have suggested an extension of the Haken-Kelso-Bunz model (Haken et al., 1985) so that the model incorporates an intrinsic attractor for the 90°-phase pattern. However, it is questionable to what extent the 90°-phase pattern is an *intrinsic* attractor. The participants in the Peck and Turvey study were offered practice specifically with this pattern before the experiment. It has been shown that practice can change the attractor layout (Schöner et al., 1992; Zanone & Kelso, 1992). In fact, the 90°-phase pattern is often used as the to-be-learned (i.e., novel) phase pattern in learning experiments using coordination tasks of a more continuous nature (Fontaine et al., 1997; Lee et al., 1995; Smethurst & Carson, 2001; Swinnen et al., 1997, 1998; Tsutsui et al., 1998; Wishart et al., 2002; Zanone & Kelso, 1992). In these tasks, the fingers, hands or arms freely oscillate in their natural anatomical boundaries. No "hard" landmarks providing rhythmic haptic and auditory feedback are available. Thus, the stability of the 90°-phase pattern depends on the nature of the coordination task.

In contrast to a view of the 90°-phase pattern as a stable intrinsic attractor, subjects may have been attracted to the 90°-phase pattern only by pacing and instruction (Geuze, 2001). This might explain why the effect of musical experience on stability was particularly strong in the gallop. Due to their musical training, musically experienced subjects may be more proficient in coupling their

movements to external or memorized information. This would imply that musical experience not only strengthens the attractors that form part of the intrinsic dynamics, but also enhances the ability to form new attractors based on behavioral information. The idea of the 90°-phase pattern as a temporary, flexible behavioral attractor is further supported by the finding that accuracy of the gallop was especially low after the switch, when no initial pacing was available. In conclusion, our study supports the idea that in finger tapping, the 90°-phase pattern value may be an arbitrary attractor.

The strong intra-individual preference for one type of gallop, in most cases the right-leading one, might be understood from a tight functional coupling between perception and action in the context of an intrinsic asymmetry (handedness) or asymmetry in behavioral information. In perception theory, the principle of proximity states that two stimuli separated by a shorter distance, in time or space, than the surrounding ones will be perceived as grouped. Research on visual (e.g., Banks & Prinzmetal, 1976) and auditory stimuli (e.g., Bregman & Reidnicki, 1975) has supplied evidence for this theoretical principle. Similarly, in the 90°-phase pattern one hand is generally perceived as leading and the other as following. Consequently, one may expect a hierarchical ordering in which the right hand (in the right gallop) or the left hand (in the left gallop) leads the other hand. Such a hierarchical organization has indeed been shown for the gallop (Verheul & Geuze, 2003). Studies on handedness and bimanual coordination (e.g., Peters, 1994; Rogers et al. 1998) have shown that the more demanding task is usually performed by the preferred hand, which also receives most attention. From these studies it can be expected that the preferred hand will coincide with the leading hand in the 90°-phase pattern. In our mainly right-handed population, this would lead to a high occurrence of the right leading 90°-phase pattern, which was indeed confirmed. A minority (one left-hander and three right-handers), however, chose the gallop in which their non-preferred hand was leading. Since handedness issues were not the focus of this study and we therefore included only two left-handed subjects, we cannot statistically test the hypothesized relationship between handedness and hand role in the 90°-phase pattern. An alternative explanation for the pre-dominance of the right-leading gallop may be the asymmetry in behavioral information. The horse animation showed a right-leading gallop. Nonetheless, this fails to explain the consistency in the neutral condition.

The distribution of hand roles also seems to play a role in the switch strategies. These strategies revealed a strong intra-individual consistency, which correlated with the choice of left or right leading 90°-phase pattern. In switches from or to this pattern, the switch strategy and choice of gallop are not independent. More informative, therefore, is the consistent use of the same strategy in the in-phase to anti-phase and anti-phase to in-phase switch conditions. This finding suggests that the functional asymmetry between the two hands also exists in symmetrical phase patterns. In the Haken-Kelso-Bunz model (Haken et al., 1985) for rhythmic bimanual coordination, the component oscillators - the left and right hand - are assumed to be symmetrical, but various researchers have pointed out small but systematic deviations from the required relative phase due to handedness in in-phase and anti-phase patterns (Stucchi & Viviani, 1993; Swinnen et al., 1996). Our results support the idea of functionally asymmetric component oscillators.

One implication of this notion is that the model described by Haken et al. (1985) should be extended or altered to incorporate a term or parameter causing symmetry breaking. Three methods have been proposed: (*i*) the addition of a detuning term to the model (e.g., Kelso & Jeka, 1992; Peck & Turvey, 1997), (*ii*) the addition of the first two odd (sine) terms of the Fourier series (Treffner & Turvey, 1996) and (*iii*) the addition of a symmetry parameter (Fuchs & Jirsa, 2000). These model extensions have been formulated to account for the effects of a difference in eigenfrequency between the oscillators, hand-preference, and asymmetric axes of rotation, respectively. They have been able to describe phenomena such as a phase shift, enhanced variability and a transition from in-phase to anti-phase. The slightly asymmetric potential that is a result of model extensions (*i*) and (*ii*) might account for a preferred 'route' (switch strategy) when switching between patterns.

In the version of the Haken-Kelso-Bunz model in which two Fourier (cosine) terms have been added to incorporate the gallop as a stable pattern (Peck & Turvey, 1997), the relative stability of the left and right leading gallop patterns is represented by the relative strength of each of the two terms. Combinations with the aforementioned model extensions can account for both the consistent choice of one type of gallop and the consistent use of one type of switch strategy. Nonetheless, these models do not explain why the choice of gallop showed a close relationship with the switch strategy (among others for the switch from in-phase to anti-phase and vice versa).

A different approach is to start from the idea of a maximally asymmetrical coupling, i.e., a uni-directional coupling. In such a coupling, one hand (the timer) would influence the movements of the other (the subordinate hand), but there would be no or less reciprocal influence (Summers et al. 1993; Verheul & Geuze, 2003). The interdependency between the hands has been investigated for anti-phase and gallop tapping (Verheul & Geuze, 2003), and a slightly but significantly asymmetrical coupling was found for the gallop, but not for the anti-phase pattern. This model could explain the consistent choice of one type of gallop, but would predict a switch strategy based on one hand (the subordinate hand) changing its timing relative to the other (the timer). The latter was not found. Rather, the switch strategy was not linked to a particular hand, but based on the effect on the relative phase (e.g., slowing down the left hand or speeding up the right was found to fall within the same switch strategy).

In conclusion, musical experience had a significant effect on coordination stability and accuracy. The manipulation of memorized behavioral information did affect coordination dynamics, but not fully in line with expectations. In particular, the effect of behavioral information on switching times cannot be fully explained. Future research should further elucidate how musical experience interacts with behavioral information (e.g., environmentally-specified) and intrinsic and task asymmetries in the rhythmical coordination of the hands.

3

"Side Effects"

Intrinsic and task-induced asymmetry in bimanual rhythmic coordination
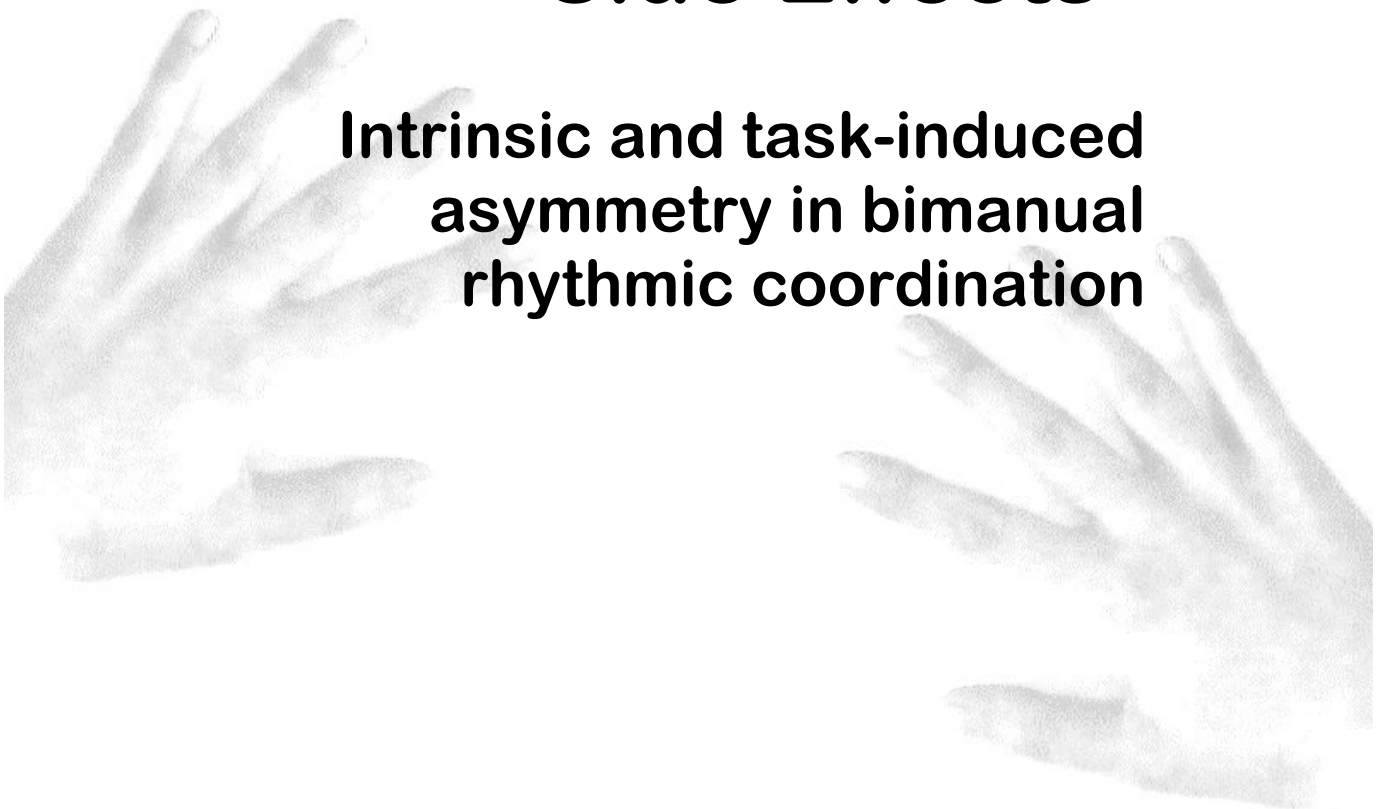
Abstract Multifrequency coordination studies have shown the importance of hand-role in addition to hand-preference in bimanual rhythmic coordination. In these studies, hand-role has been defined by the task of the individual hands (fast or slow). In the present study, the hands were coordinated at the same frequency and hand-role was defined by the asymmetry of the coordination pattern. Eleven consistent left-handers and thirteen consistent right-handers tapped three patterns (anti-phase, left-gallop, right-gallop) in four visual feedback conditions (no feedback, left-hand feedback, right-hand feedback, full feedback). The analysis focused on phase shifts, phase variability, intertap interval variability and correlations between intertap intervals. The manipulation of visual feedback had only minor effects. In the anti-phase pattern, a symmetric coupling mechanism was found. The results support the idea that coordination in the gallop pattern is governed by a hierarchical control mechanism. In contrast to the multifrequency studies, however, successful control in the gallop is not dependent on a hand arrangement that accommodates the preferred hand as the leading hand. An adjustment to the model of Summers et al. (1993) is presented for the case of the gallop pattern.

3.1 Introduction

Many of the everyday bimanual tasks that we perform are asymmetric in nature. The preferred hand usually performs the task that is directly related to the goal (for example, lighting a match) while the non-preferred hand supports that task (for example, holding the box, Guiard, 1987). The strong interaction between task asymmetry (hand-role) and intrinsic asymmetry (hand-preference / cerebral dominance) on task performance becomes instantly clear when the hand arrangement is reversed. Usually, this has a detrimental effect on task performance. The same phenomenon has been shown in rhythmic coordination, in so-called multifrequency patterns, in which the two hands move rhythmically at two different frequencies. For instance in the 2:3 frequency pattern, a preference was found in right-handers to use the right hand as the faster limb (Peters & Schwartz, 1989). It has consistently been shown, at least for right-handers, that this type of distribution of hand-roles is also the most successful (Byblow & Goodman, 1994; Peters, 1981; Peters, 1994). Although these results are not conclusive in the absence of a left-handed group, together they suggest that there is an optimal hand arrangement that is related to hand-preference.

3.1.1 *Hand-role*

A hierarchical control mechanism for multifrequency coordination that is based on hand-role rather than hand-preference was proposed by Summers et al. (1993). They studied a series of polyrhythms (3:2, 5:2, 4:3, 5:3 and 5:4) performed by right-handers in both hand arrangements (i.e., the right hand took the faster beat and the left hand the slower beat, and vice versa). The analysis of correlations between adjacent between-hand intertap intervals and within-hand intertap intervals revealed a hierarchical control in which the beats produced by the fast hand are used as a time base for interlacing the beats produced by the slow hand. This model is supported by subsequent studies focusing on multifrequency patterns. Byblow and Goodman (1994) studied a 2:1 coordination task with an increasing frequency paradigm. All bifurcations to a 1:1 coordination occurred through the slow forearm increasing its speed to equal the speed of the fast forearm, revealing the forcing nature of the faster arm. In skilled drummers, Peper et al. (1995a) determined the degree of harmonicity, other than the actual tapping frequency, in the power spectrum of each hand in a 2:3 coordination task, and in

unimanual conditions. The results indicated an almost unidirectional influence of the fast hand on the slow hand. No effect of hand arrangement was found on this control mechanism in any of these studies.

In sum, in multifrequency tasks a hierarchical coupling mechanism was found, in which the hand tapping the faster beat is leading (or forcing) and the hand tapping the slower beat interlaces its taps at a certain interval after one or more of the faster beats in each cycle of the repeating pattern. This hierarchical coupling is fully dependent on the task assigned to the hand (i.e., hand-role) and not on hand-preference. When the non-dominant hand taps with the highest frequency, it automatically takes on the forcing hand-role. However, coordination deteriorates markedly in this hand arrangement.

Although the studies mentioned above stress the importance of hand-role (in addition to hand-preference), it remains unclear what aspect of the task-asymmetry is causing the effects reported. In multifrequency coordination patterns, the two hands tap with different frequencies, which clouds the distinction between the effects of asymmetry in speed and coupling. The present study investigates whether asymmetry in the phase relation alone is characterized by a similar hierarchical control mechanism as identified for multifrequency patterns and if so, whether coordination deteriorates when the non-preferred hand takes on the leading hand-role.

To answer these questions, we studied bimanual tapping in a gallop pattern. In this pattern both hands tap at the same frequency but one hand taps a quarter of a cycle ahead of (or after) the other (i.e., 90° or 270° out-of-phase coordination). Thus, asymmetry exists only in the phase relation. As a result of the broken symmetry (Stewart & Golubitsky, 1992), the gallop has two configurations. Two events separated by a short distance in space (visual) or time (auditory) tend to be perceived as a group (perception theory; Banks & Prinzmetal, 1976; Bregman & Reidnicki, 1975). Similarly, in the gallop pattern the two taps separated by a quarter of a cycle tend to be perceived as a group and the hand that is a quarter of a cycle ahead is generally perceived as leading the other. For practical purposes we will call the type of gallop in which the left hand is a quarter of a cycle ahead the *left-gallop*, and the reverse pattern the *right-gallop*. A hierarchical ordering in which the right hand (in the right-gallop) or the left hand (in the left-gallop) leads the other hand is expected.

In Figure 3.1, an adaptation of the model proposed by Summers et al. (1993: Fig. 2) is presented for the case of the gallop. From this model, we can deduce

several specific predictions. The first prediction is directly related to the calculation of the *relative phase*, a variable quantifying coordination between the hands. If the model is correct, then it is the "intention" of the participant in a right-gallop to place a left-hand tap at a quarter of a cycle of the right hand, rather than to place a right-hand tap at three-quarters of a cycle of the left hand. In other words, the relatively independent "units" are right-hand intertap intervals with left-hand taps placed inside that interval. If the calculation of the relative phase reflects this hierarchical ordering, variability will be lower than when a calculation is used that does not reflect this hierarchy. Of course, the reverse would be true for the left-gallop (*prediction 1*). Similarly, the variability of intertap intervals should reflect the hierachical organization. In particular, intervals of the leading hand are expected to be more stable than intervals of the non-leading hand (*prediction 2*). The third set of predictions of the model concerns the inter-dependency between adjacent intertap intervals, both between and within hands. Following from the model, the timing of the leading hand should be indifferent to variations in the timing of the non-leading hand, whereas the timing of the non-leading hand should be dependent on the timing of the leading hand (*prediction 3*). Summers et al. (1993) called these the *interhand dependency predictions.* A comparison of correlations between adjacent intervals can reveal the direction of the dependency between the hands.

The last prediction concerns the dependency between adjacent taps within each hand. According to a model originally developed for one-handed rhythmic tapping by Wing and Kristofferson (1973) and adjusted for two-handed tapping by Turvey et al. (1989), tapping variability within each hand can be divided into so-called 'clock' and 'motor' variability. The first type of variability is ascribed to natural variability in the timekeeper and the second type of variability is due to variability in the motor delay. The relative contribution of each can be identified by determining the lag 1 autocorrelation for a series of taps. A correlation of 0 would indicate a large timekeeper variance. A negative correlation would indicate that motor variance has contributed significantly to the over-all variance. The model predicts a lower timekeeper variance in the leading hand than in the non-leading hand and therefore a more negative correlation between taps of the leading hand than taps of the non-leading hand (*prediction 4*).
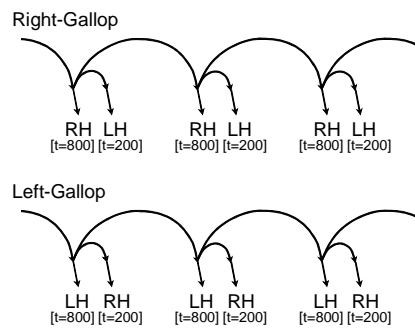
Figure 3.1 The hierarchical control model as proposed by Summers et al. (1993) adapted for the gallop, tapped at 1.25 Hz (i.e., cycle duration 800 ms). The timing of the non-leading hand is subordinated to the timing of the leading hand. *RH* right hand, *LH* left hand.

3.1.2 *Interaction hand-role and hand-preference*

The deterioration in performance in the non-preferred hand arrangement, found consistently in multifrequency studies, may be the result of the hierarchical control mechanism described above or of the asymmetry in frequency between the hands. If the deterioration is a direct effect of the hierarchical mechanism, and if such a mechanism is underlying the gallop, it will be present in the gallop as well. In the bimanual and bipedal gallop, a strong preference has been found in right-handers to use the right hand (Verheul & Geuze, 1999) or leg (Whitall & Caldwell, 1992) as the limb that is a quarter of a cycle ahead of the other limb. However, none of the studies on the bimanual gallop (e.g., Fontaine et al., 1997; Geuze, 2001; Lee et al., 1995; Peck & Turvey, 1997; Verheul & Geuze, 1999; Zanone & Kelso, 1992) systematically compared both hand-role distributions (i.e., left-gallop, right-gallop). In the present study, the effects of hand arrangement on the stability of performance will be determined for both the performance of the individual hands and the coordination between them.

A consequence of the hierarchical model is that hand-preference has no effect on the relative stability of the hands *within* one type of gallop. The leading hand is

expected to be more stable than the non-leading hand, regardless of hand-preference.

However, this does not necessarily imply that the non-preferred hand gains stability when forced into the leading hand-role. If the deterioration of performance in multifrequency coordination is related to the hierarchical coupling, then a hierarchical control in the gallop will also coincide with a difference in performance between the two hand arrangements. The superior performance of the non-preferred hand in the non-preferred type of gallop would then be due to a substantial decrease in the performance level of the preferred hand. If, however, the deterioration of performance in multifrequency patterns is related to the asymmetry in tapping frequencies, the gallop may show a hierarchical coupling mechanism without the interaction with hand-preference. In this case, successful control in the gallop will not depend on a hand arrangement that accommodates the preferred hand as the leading hand, and the non-preferred hand is likely to gain stability when forced into a leading hand-role.

3.1.3 *Hand-preference*

If results do not support the hierarchical coupling (hand-role) model for the gallop pattern, the underlying mechanism may be a hierarchical coupling based on hand-preference instead of hand-role or a symmetric coupling that may be influenced by hand-preference. The former model is similar to the hierarchical model presented above, but with hand-preference as the basis for hierarchy rather than hand-role. The movements of the non-preferred hand are in this model subordinate to the movements of the preferred hand. The latter, symmetric, model has been proposed as the mechanism underlying simultaneous (in-phase) and alternating in 180° phase relation (anti-phase) coordination (see, for example, Treffner & Turvey, 1996). These patterns have been studied extensively over the years (for an overview, see Kelso, 1998), but no complete correlation analysis has been done to test the hierarchical model presented earlier. Haken et al. (1985) have shown that a model of two symmetrically coupled oscillators successfully describes the spontaneous tendencies found in in-phase and anti-phase limb coordination. Important assumptions of the model are that the oscillators, i.e., the limbs, and the coupling between them, are symmetrical. As a consequence, the model predicts no asymmetries in the performance of the individual hands or in the phase relation. Over the last two decades, however, it has been recognized that

hand-preference has a small, but systematic effect on in-phase and anti-phase coordination. In bimanual rhythmic tasks such as circle drawing and pendulum swinging, individuals show a small, but systematic deviation from the in-phase and anti-phase patterns. Most commonly the preferred hand is slightly ahead of the non-preferred hand (Amazeen et al., 1997; Stucchi & Viviani, 1993; Treffner & Turvey, 1995). Swinnen et al. (1996) found this asynchrony in right-handers, but not in left-handers. This effect of hand-preference on in-phase and anti-phase coordination has been captured in an extension of the Haken-Kelso-Bunz model (Treffner & Turvey, 1996). The preferred hand was also found to be less variable than the non-preferred hand during in-phase and anti-phase tasks (see, for example, Riek et al., 1992; Rogers et al., 1998; Wuyts et al., 1996). In a bimanual circle drawing task, trajectory distortions and movement direction reversals were observed only in the non-preferred hand (Semjen et al., 1995). Thus, despite the symmetry of the task, asymmetries related to hand-preference are observed both in the performance of individual hands and in the coordination between the hands.

The gallop shows the same coordination dynamics as the in-phase and anti-phase patterns under the manipulation of cycle frequency (Geuze, 2001) and eigenfrequency of the oscillators (hand-held pendulums; Peck & Turvey, 1997). If the mechanism underlying the gallop is similar to the one underlying in-phase and anti-phase co-ordination, one may expect a phase shift in the direction of the preferred hand (*prediction I*) and a difference in stability between the hands directly related to hand-preference *(prediction II)*. The present study will investigate the effects of hand-preference on the phase shift and the intertap interval stability of both hands in both types of the gallop and the anti-phase pattern.

3.1.4 *Attention*

In the literature, both hand-preference and hand-role have been related to the allocation of attention (e.g., Peters, 1994; Summers et al., 1993). The preferred hand is believed to receive continuous, "on-line" attention, whereas the non-preferred hand receives attention of a more intermittent quality (Corballis, 1989; Peters, 1994). Under normal everyday conditions, the preferred hand is the leading hand and receives more attention.

The effect of explicitly directing attention to the preferred or non-preferred hand in symmetric coordination tasks was investigated in several studies, with

inconsistent results. Swinnen et al. (1996) and Amazeen et al. (1997) instructed subjects to direct their attention to one of the hands and visually monitor its movements. They observed larger phase shifts and lower relative phase variability in both left- and right-handed subjects when they directed their attention to the preferred hand than when they directed their attention to the non-preferred hand. Stucchi and Viviani (1993) found no effect of directing attention in a bimanual circle drawing task. This may have been due to the use of sound instead of vision to direct attention. Directed attention also seems to have an effect on single hand performance in bimanual coordination tasks (Rogers et al., 1998; Swinnen et al., 1996; Wuyts et al., 1996). The difference in consistency between limbs increased when subjects monitored the dominant limb and decreased when they monitored the non-dominant limb. Note that both the phase shift and the asymmetry between the hands were changed but not reversed when the direction of attention was reversed. In multifrequency coordination patterns, interactions between attention and hand-role and/or hand-preference have been reported (Byblow & Goodman, 1994; Peters & Schwartz, 1989; Peper et al., 1995b). No studies have reported on the effects of attentional manipulations in the gallop.

In the present study, the effects of, and interactions between, intrinsic asymmetry and task asymmetry on bimanual coordination were evaluated. More specifically, we investigated whether different hand-roles can be identified in the gallop (*predictions 1 to 4*) and if so, whether the distribution of hand-roles is associated with a difference in performance between the two configurations of the gallop pattern, analogous to the multifrequency patterns. We also investigated two alternative models. Firstly, a hierarchical coupling model based on hand-preference was tested, involving the same 4 predictions with hand-preference taking the place of hand-role. Secondly, two predictions of a symmetric coupling model were tested (*predictions I and II*). In this case, the preferred and non-preferred hand do not take on hierarchically different roles, but hand-preference 'shines through' as a small phase shift and differential stability between the two hands. These latter two models were also evaluated for the anti-phase pattern. The anti-phase pattern was included in the present study in order to confirm that this coordination pattern showed no sign of a hierarchical control. Finally, we investigated the interaction effects of hand-preference and hand-role with directed attention.

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To investigate these issues, a group of left-handers and a group of right-handers tapped the gallop in its two different modes (right- and left-gallop) and the anti-phase pattern. To manipulate the focus of attention, we introduced two asymmetric visual feedback conditions (feedback from the left or right hand), as well as two symmetric control conditions (no feedback, full feedback).

3.2 Methods

3.2.1 *Subjects*

Subjects were recruited from the student population. A hand-preference questionnaire (Van Strien, 1992; Van Strien & Bouma, 2000, see Appendix I) was used to select consistent right-handers and left-handers. This questionnaire is based on the most reliable and valid items selected from several handedness questionnaires (Annett, 1970; Oldfield, 1971; Raczkowski et al., 1974). Subjects answered ten questions related to the use of their hands in specific tasks. A score of –1 was given to each item that was answered with "left", +1 to each item answered with "right" and 0 to each item answered with "both". A total score of -10 indicates extreme left-handedness and +10 extreme right-handedness. Subjects with scores below –5 were assigned to the left-handed subgroup and subjects with scores above +5 to the right-handed subgroup. The left-handed subgroup consisted of 11 subjects (mean age 24 yrs., SD 4.1 yrs.; 4 men, 7 women), with handedness scores -6 (n=1), -8 (n=4) and -10 (n=6). The right-handed subgroup consisted of 13 subjects (mean age 23 yrs., SD 2.6 yrs.; 5 men, 8 women) with scores +7 (n=1), +9 (n=2) and +10 (n=10). All subjects gave their written informed consent prior to participation. The study was approved by the local ethics committee.

3.2.2 *Apparatus*

Two touch-sensitive buttons (diameter 2.5 cm, 7.5 cm apart) that were built into the slanted surface of a box (30 x 20 x 2 to 6 cm) were used to register finger taps. The fingers produced a slight sound when they touched the buttons. The box also served as a support for the hands. Visual feedback was manipulated by an adjustable black plate that was situated above the hands, but did not restrict their movements.

3.2.3 *Procedure*

Subjects were seated in a comfortable chair at a table. Subjects were asked to tap with their index fingers on the buttons, while their hands and remaining fingers rested on the box with their arms on the table surface throughout each trial. Before the beginning of each trial, the experimenter told the subject which pattern to tap and reminded him/her to watch the visible hand or hands carefully. During the first 6 cycles of each trial both hands were paced (PC generated acoustic beeps lasting 75 ms), specifying 180° or 90° phasing between the hands. The frequency of the initial pacing was 1.25 Hz for each finger. Subjects were instructed to continue tapping as constantly as possible after the pacing stopped until the signal to stop was given by the experimenter after 21 non-paced cycles. Three patterns were tapped: anti-phase, left-gallop and right-gallop. Each pattern was tapped twice in each of four visual feedback conditions: no feedback, left-hand feedback, right-hand feedback and full feedback from both hands. This resulted in a total of 24 bimanual tapping trials per subject, administered in eight blocks of three trials. In each block, the visual feedback condition was held constant and the three patterns were tapped in randomized order. Between blocks, the visual feedback condition was changed in such a way that each feedback condition was administered twice. The experimenter demonstrated each pattern. One practice trial for each pattern was given with full visual feedback.

3.2.4 *Data reduction*

Only the self-paced parts of the trials were analyzed. The parameter describing coordination is the relative phase (ϕ), calculated in this study in two ways:

$$\phi = (L_n - R_n)/(R_{n+1} - R_n) \times 360° \qquad (1)$$
$$\phi = (R_n - L_n)/(L_{n+1} - L_n) \times 360° \qquad (2)$$

in which L and R are the points in time at which the left and right index finger hit the button. The first calculation reflects a hierarchical model in which the right hand is leading, the second reflects a model in which the left hand is leading. For

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each trial, variability of the relative phase (i.e., standard deviation) during self-paced tapping was calculated twice, once with each equation for the relative phase. The phase shift was calculated as the average deviation from the required relative phase in each trial, and was calculated twice as well. A negative phase shift on the basis of equation 1 means that the left hand is tapping too early in each cycle, whereas a positive phase shift means that the right hand is advanced. The opposite is the case for equation 2, so a sign inversion was applied to the outcomes of equation 2, so that, in all cases, a positive phase shift indicated that the right hand tapped too early, and a negative phase shift indicated that the left hand tapped too early. The variability of intertap intervals (ITI) (i.e., standard deviation) was calculated for each hand. Finally, Pearson's product-moment correlation coefficients were calculated for adjacent within-hand intervals (LL-LL and RR-RR) and between-hand intervals (LR-RL and RL-LR, Figure 3.2).

Figure 3.2 Schematic of the intertap intervals that were correlated. Lag 1 autocorrelations were calculated for adjacent within-hand intervals (LL-LL and RR-RR) and between-hand intervals (LR-RL and RL-LR). *L* left hand tap, *R* right hand tap.
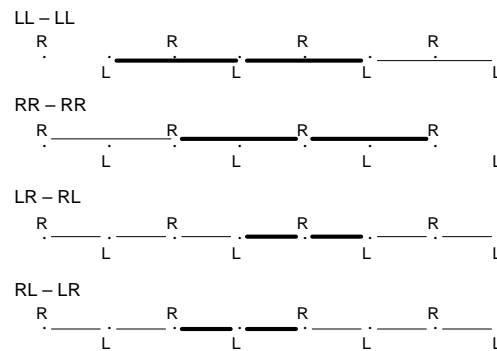
3.2.5 *Statistical analysis*

Repeated measures ANOVAs were performed on the data. Separate analyses were performed for the gallop and anti-phase patterns, in order to test for each of

these patterns whether a hierarchical coupling could be identified. In the gallop, this hierarchical coupling could be based on hand-role or hand-preference. Since the anti-phase pattern is a symmetrical pattern (i.e., it has only one configuration), a hierarchical organization in this pattern would be based on hand-preference. The alternative model of a symmetrical coupling, influenced by hand-preference, was also tested for both the gallop and the anti-phase pattern. In addition to evaluating the three main models, we also tested whether performance was superior when hand arrangement in the gallop was such that the preferred hand was leading, i.e., whether hand-role interacted with hand-preference. Finally, the effect of the four attention conditions was investigated.

To test our hypotheses about the gallop, the following repeated measures ANOVAs were performed: hand-preference (2) x gallop pattern (2) x equation (2) for relative phase variability (this was only used to test prediction 1), hand-preference (2) x gallop pattern (2) x attention (4) for phase variability and phase shift (for each phase equation separately), and hand-preference (2) x gallop pattern (2) x attention (4) x hand / interval-pair (2) for intertap interval variability and correlation. "Hand" was a variable used in the analysis of intertap interval variability, "interval-pair" refers to the analysis of the correlation between adjacent intervals, between hands (RL-LR and LR-RL) or within hands (RR-RR and LL-LL). For the anti-phase, the same analyses were performed without the independent variable 'gallop pattern'. Finally, the anti-phase and gallop patterns were compared in analyses containing all three patterns.

The significance level α was set at .05. When the assumption of sphericity was violated, the conservative Greenhouse-Geisser method was used to correct the degrees of freedom for the tests of significance. This is indicated in the text by "GG". In the results section, to facilitate reading, only statistical details of significant effects are given. For significant main effects of variables with more than two levels, post hoc pair-wise multiple comparisons were performed with Bonferroni adjustment. For significant three-way interaction effects, post hoc simple interaction effects were calculated, i.e., interaction effects between two of the variables at all levels of the third. For significant simple interaction effects that were more complex than 2 x 2 levels, pair-wise multiple comparisons were subsequently performed (again, with Bonferroni adjustment). This method prevents inflation of the *per family* type I error rate, while maintaining power of individual pair-wise comparisons. In the results section, we focus on the predictions, mainly two-way interaction effects (e.g., gallop pattern x equation,

gallop pattern x interval-pair, gallop pattern x hand, hand-preference x equation, etc.). However, all other significant effects are reported as well.

3.3 Results

The results will be presented following the order of the predictions from the Introduction section.

3.3.1 *Gallop*

3.3.1.1 *Hand-role*

In contrast to the first prediction, the two relative phase equations did not generate significantly different values for the relative phase variability in interaction with gallop pattern. Average standard deviations of the relative phase were 9.2° and 9.4° (equation 1) and 9.4° and 9.1° (equation 2), for left- and right-gallop respectively.

In concordance with the second prediction, a significant interaction between gallop pattern and hand was found for the variability of intertap intervals in the gallop ($F(1, 22)=17.26$, $p<.001$). In the left-gallop, the left hand was less variable than the right hand, whereas in the right-gallop, the right hand was less variable than the left hand. A significant interaction between pattern, hand and hand-preference ($F(1, 22)=5.28$, $p<.05$) indicated that this effect was different for right-handers and left-handers. Figure 3.3 shows this interaction-effect. Post hoc tests of the simple interaction effects showed that the interaction effect between pattern and hand was significant in right-handers (*dotted lines*, $F(1, 12)=19.72$, $p<.005$). In the right-gallop, variability was decreased in the right hand and increased in the left hand compared to the left-gallop (mean values; right hand: 30.9 ms in right-gallop and 34.7 ms in left-gallop; left hand: 35.9 ms in right-gallop and 31.6 ms in left-gallop). In left-handers, the interaction between pattern and hand was not significant (*solid lines*). In this group, both the left and the right hand were more variable in the right-gallop than in the left-gallop (right hand: 31.6 ms in right-gallop and 30.8 ms in left-gallop; left hand: 33.2 ms in right-gallop and 30.0 ms in left-gallop). The switch in most stable hand, when comparing the two gallop patterns, was due to a larger change in variability in the left than in the right hand.
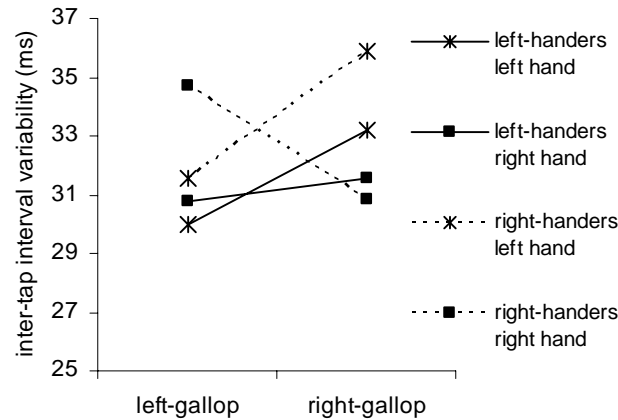
Figure 3.3 Variability of intertap intervals of the left and right hand in both types of gallop for left- and right-handers separately. In right-handers, the non-dominant hand (the left hand) gains stability when the leading hand-role is imposed upon it by the task (the left-gallop).

The interhand dependency predictions (prediction 3) were tested using the correlation patterns between adjacent *between-hand* intervals. Correlations for all three patterns are summarized in Table 3.1. For the adjacent between-hand intervals, a significant interaction was found between gallop pattern and interval-pair ($F(1, 22)=12.54$, $p<.01$). In the left-gallop, the correlation between intervals LR and RL was stronger than the correlation between intervals RL and LR, whereas in the right-gallop, the correlation between intervals RL and LR was stronger than the correlation between intervals LR and RL. These results indicate that in the left-gallop, the timing of the right hand is more dependent on the timing of the left hand than vice versa, whereas for the right-gallop, the reverse is true.

The relative contribution of clock and motor variability for each hand can be deduced from the correlation patterns between adjacent intertap intervals *within* each hand. These lag 1 autocorrelations for within-hand intervals were extremely low in the gallop (approximately 0, see Table 3.1). This means that the contribution of negatively correlated motor variance, relative to the contribution of clock variance, was extremely low. In contrast to prediction 4, no significant interaction between type of gallop and hand was found that would indicate a

distinctly higher contribution of negatively correlated motor variance to over-all variance in the left- or right-hand taps related to type of gallop.

Table 3.1 Correlations between adjacent intertap intervals, between hands and within hands (see Fig. 2).

	Correlated Intertap Intervals			
	Between hands		Within hands	
Pattern	RL – LR	LR – RL	RR – RR	LL - LL
Anti-phase	-.16	-.16	-.15	-.14
Left-gallop	-.20	**-.29**	<u>-.05</u>	<u>-.03</u>
Right-gallop	**-.29**	-.17	<u>-.02</u>	-.08

Note. Calculated per trial, averaged per subject, then averaged over subjects. Post hoc pair-wise comparisons for all pairs in this diagram revealed significant differences ($p<.05$) between the numbers in bold and the numbers that are underlined.

3.3.1.2 *Interaction Hand-role and Hand-preference*

No significant interaction was found between gallop pattern and hand-preference for relative phase variability that would indicate a decrement in performance related to hand-arrangement in the gallop. Similarly, no significant interaction was found between phase pattern and hand-preference for intertap interval variability.

As mentioned above, a significant three-way interaction between gallop pattern, hand-preference and hand was found for intertap interval variability ($F(1, 22)=5.28$, $p<.05$). This effect might indicate that there is a significant interaction effect between gallop pattern and hand-preference for either the left or right hand. This would be revealed in figure 3.3 by the lines for the left hand or right hand not being parallel. The figure suggests that there may be such an effect in the right hand. However, post hoc analyses of this two-way interaction for each hand separately showed that, for both hands, the interaction between phase pattern and hand-preference was not significant.

3.3.1.3 *Hand-preference*

A *hierarchical model* based on hand-preference instead of hand-role was evaluated with tests equivalent to the ones described in the first paragraph of this section, but with gallop pattern substituted by hand-preference. No significant

interaction was found between hand-preference and relative phase equation for phase variability. The average phase variability was 8.8° for left-handers and 9.7° for right-handers according to equation 1, and 8.7° and 9.8° for left- and right-handers according to equation 2. However, a significant three-way interaction between hand-preference, the phase equation and the attention condition was found. Post hoc analysis of the interaction between hand-preference and the phase equation at each level of the attention condition showed a significant interaction in the condition in which both hands were covered (F(1, 22) = 5.97, *p*<.05). In this condition, right-handers had a lower average phase variability than left-handers according to equation 1, but a higher average phase variability according to equation 2. Thus, the predicted interaction was found only in the condition in which no visual feedback from the hands was available.

No significant interaction was found between hand-preference and hand for the intertap interval variability. Average interval variability of the left hand was 32 ms in left-handers and 34 ms in right-handers. Similar values were obtained for the right hand; 31 and 33, for left- and right-handers, respectively. However, as mentioned above, a significant interaction effect between hand-preference, hand and pattern was found. This might indicate that there is a significant interaction between hand-preference and hand in one of the gallop patterns, but not in the other. A post hoc analysis tested the interaction between hand-preference and hand for each pattern separately. Results showed that this interaction was significant in the left-gallop (*F*(1, 22)= 4.37, *p*<.05), but not in the right-gallop. In the left-gallop, as can be seen in Figure 3.3, the left hand was on average more stable than the right in both left- and right-handers. The significant interaction indicates that the difference in variability between the hands was substantially larger in right-handers than in left-handers. Thus, this interaction does not support a hierarchical model based on hand-preference. The preferred hand was not significantly more stable than the non-preferred hand.

No significant interaction was found between hand-preference and interval-pair for the correlation between adjacent between-hand intervals (interhand dependency). The average correlation between adjacent RL-LR intervals was -.23 for left-handers and -.26 for right-handers, the average correlation between adjacent LR-RL intervals -.21 in left-handers and -.25 in right-handers. However, a significant three-way interaction was found between hand-preference, interval-pair and directed attention (*F*(3, 66)=5.25, *p*<.01). Post hoc testing of simple interaction effects at each level of the attention factor revealed a significant

interaction between hand-preference and interval-pair when both hands were covered ($F(1, 22)=12.94$, $p<.005$). In this condition, higher negative correlations were found for the interval-pairs between two taps of the non-preferred hand (i.e., RL-LR in left-handers, LR-RL in right-handers; both -.32 on average), than for the interval-pairs between taps of the preferred hand (i.e., LR-RL in left-handers (-.15), RL-LR in right-handers (-.22)). This indicates that the timing of the preferred hand was more dependent on the timing of the non-preferred hand than vice versa, in this particular attention condition. This suggests a hierarchically superior role for the non-preferred hand, a finding that is clearly not in line with the model tested here.

Finally, no significant effect was found between hand-preference and interval-pair for the correlation between adjacent within-hand intervals (relative contribution of clock and motor variance). Average values for lag 1 autocorrelations RR-RR and LL-LL were very similar for left-handers and right-handers (RR-RR: -.04 and -.03; LL-LL: -.06 and -.05, respectively).

In contrast to the predictions based on a *symmetric coupling influenced by hand-preference,* no significant main effect of hand-preference was found for the phase shift. Left-handers showed an average phase shift of -0.1° (equation 1) or -0.2° (equation 2). Right-handers showed an average phase shift of -0.3° (equation 1) or -0.5° (equation 2). Neither did we find a significant interaction of pattern with hand-preference. Instead, a main effect of gallop pattern was found. The phase shift differed significantly between the two gallop patterns ($F(1, 22)= 11.66$, $p<.01$ (equation 1) and $F(1, 22)=12.29$, $p<.01$ (equation 2)). The left-gallop showed a negative phase shift (-8.4.° equation 1 and -8.7° equation 2) indicating that the left hand was on average tapping too early in the cycle. The right-gallop showed a positive phase shift (7.9° equation 1 and 8.1° equation 2) indicating that the right hand was tapping too early.

Also in contrast to a symmetric coupling model for the gallop, hand-preference showed no interaction effect with hand for intertap interval variability. This finding was already mentioned in relation to the hierarchical model based on hand-preference (second paragraph of this section). Referring to the same paragraph, the three-way interaction between hand-preference, hand and pattern for intertap interval variability was shown *not* to indicate that the preferred hand was more stable than the non-preferred hand in one of the gallop patterns.

3.3.2 *Anti-phase*

In contrast to the *hierarchical model*, no significant interaction was found between hand-preference and the equation used for calculation of the relative phase for phase variability in the anti-phase pattern. The average phase variability was 7.3° for left-handers and 7.7° for right-handers according to equation 1, and 7.6° and 7.5° for left- and right-handers according to equation 2. Neither was a significant interaction found between hand-preference and hand for the intertap interval variability. Average interval variability of the left hand was 27 ms in left-handers and 28 ms in right-handers. Values were similar for the right hand; 28 and 27, for left- and right-handers, respectively. Finally, no significant interaction was found between hand-preference and interval-pair for the correlation between adjacent between-hand intervals (interhand dependency), and the correlation between adjacent within-hand intervals (relative contribution of clock and motor variance). The average correlation between adjacent RL-LR intervals was -.13 for left-handers and -.18 for right-handers, the average correlation between adjacent LR-RL intervals -.16 in left-handers and right-handers. Average values for lag 1 autocorrelations RR-RR and LL-LL were also very similar for left-handers and right-handers (RR-RR: -.16 and -.14 ; LL-LL: -.15 and -.13, respectively).

To test the predictions based on a *symmetric coupling* influenced by hand-preference, we focused on the phase shift and intertap interval variability. Left-handers showed a significantly larger phase shift than right-handers ($F(1, 22)=4.88$, $p<.05$ (equation 1) and $F(1, 22)=5.51$, $p<.05$ (equation 2)). Left-handers were tapping too fast with the right hand within each cycle (average phase shift 1.7° according to equation 1 and 1.6° according to equation 2), whereas right-handers showed hardly any phase shift (average 0.0° according to equation 1 and -0.2° according to equation 2). Although hand-preference has an effect on the average relative phase, the absence of a phase shift in right-handers and the direction of the phase shift in left-handers are not in line with the model. Also in contrast to a symmetric coupling model for the anti-phase, hand-preference had no interaction effect with hand for intertap interval variability. As mentioned above, the preferred hand was not significantly more stable than the non-preferred hand in the anti-phase pattern.

3.3.3 *Anti-phase and gallop: the complete data set*

The anti-phase pattern differed significantly from the gallop patterns with regard to all of the dependent variables in this study. Firstly, phase pattern had a significant effect on the phase shift ($F(1.04, 22.88)=11.48$, $p<.01$ GG (equation 1) and $F(1.04, 22.87)=12.10$, $p<.01$ GG (equation 2)). Post hoc tests revealed significant differences between anti-phase and both the left-gallop ($p<.005$ equations 1 and 2) and the right-gallop ($p<.05$ equations 1 and 2), as well as between the left- and right-gallop ($p<.01$, equations 1 and 2). The phase shift in the anti-phase was on average 0.8° according to equation 1 and 0.6° according to equation 2. Phase pattern also had a significant effect on relative phase variability ($F(2, 44)=11.11$, $p<.001$ (equation 1) and $F(2, 44)=7.40$, $p<.01$ (equation 2)). Post hoc tests revealed significant differences between anti-phase and left-gallop ($p<.01$ equation 1; $p<.005$ equation 2) and between anti-phase and the right-gallop ($p<.001$ equation 1; $p<.01$ equation 2), but not between the left- and right-gallop. Average phase variability in the anti-phase was 7.5° according to equation 1 and 7.6° according to equation 2.

Variability of intertap intervals was significantly lower in the anti-phase pattern than in the gallop patterns (main effect pattern $F(2, 44)=11.10$, $p<.001$). Again, post hoc tests showed significant differences between the anti-phase and both the left-gallop ($p<.01$) and the right-gallop ($p<.001$), but not between the gallops. On average, the standard deviation of the intertap intervals was 27 ms in the anti-phase, compared to 32 ms in the left-gallop and 33 ms in the right-gallop.

Phase pattern also had a significant effect on the correlation between adjacent between-hand intervals ($F(2, 44)=4.83$, $p<.05$). Post hoc tests revealed a significant difference between anti-phase and left-gallop ($p<.05$), but not between anti-phase and right-gallop, or between the gallops. Both correlations (i.e., RL-LR and LR-RL) were -.16 on average in the anti-phase pattern. Finally, phase pattern had a significant effect on lag 1 autocorrelations for within-hand intervals ($F(1.58, 34.70)=9.20$, $p<.01$ GG). Post hoc tests revealed significant differences between anti-phase and left-gallop ($p<.005$) and between anti-phase and the right-gallop ($p<.05$), but not between the gallops. These correlation values were very similar to the values for between-hand intervals (RR-RR -.15 and LL-LL -.14 on average).

Interaction effects that were found in this complete analysis largely confirmed the earlier mentioned effects for both gallop patterns and for the anti-phase.

Firstly, for the intertap interval variability, significant interaction-effects were found between pattern and hand (F(2, 44)=11.93, $p<.001$) and between pattern, hand and hand-preference (F(2, 44)=3.63, $p<.05$). Also, the interaction effect of pattern and interval-pair for the correlation between adjacent between-hand intervals, that was reported for the gallop alone earlier, was still significant in the complete data set (F(2, 44)=7.82, $p<.01$). The same was the case for the interaction effect of hand-preference, interval-pair and directed attention for the same correlation (F(3, 66)=4.10, $p<.05$). Only the effect of hand-preference on phase shift that was found for the anti-phase data-set, was not found as a main effect or (what would have been more likely) as an interaction-effect between hand-preference and pattern in the complete data set.

One test revealed new insight into the data. A significant interaction effect was found between pattern, hand-preference and directed attention for the correlation between adjacent within-hand intertap intervals (LL-LL and RR-RR) (F(6, 132)=2.42, $p<.05$). This effect does not follow from any of the previously discussed effects for the gallop or anti-phase separately; it was not present in these separate data-sets. Post hoc tests showed that the interaction between pattern and directed attention was not significant for left-handers or right-handers separately, but the interaction between hand-preference and pattern was significant in the condition in which both hands were covered (F(2, 44)=5.895, $p<.010$). In this condition, in left-handers, adjacent intervals were on average negatively correlated in the right-gallop and anti-phase, but positively correlated in the left-gallop, whereas in right-handers adjacent intervals were on average negatively correlated in the left-gallop and anti-phase, but positively correlated in the right-gallop (Fig. 3.4). Thus, when both hands were covered, the contribution of motor variance to the over-all variance was higher in the anti-phase and right-gallop in left-handers, and in the anti-phase and left-gallop in right-handers. Note that the interaction between the gallop patterns alone (i.e., without the anti-phase pattern) did not reach significance. Post hoc pair-wise comparisons revealed no significant differences between pairs of means.

3.3.4 *Attention*

Attention had no significant main effects on, or two-way interaction effects with, any of the dependent variables in this study. The only significant effects of attention were the three three-way interaction effects that have been mentioned before.
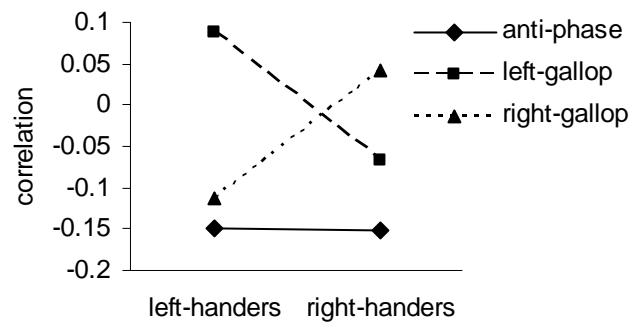
Figure 3.4 Two-way interaction between hand-preference and phase pattern for the correlation of adjacent within-hand intervals, in the condition in which both hands were covered.

3.4 Discussion

3.4.1 *Gallop*

This study investigated whether a hierarchical control mechanism (see Figure 3.1) underlies coordination in the bimanual gallop. Our findings provide evidence for such a control mechanism. As predicted by the model, the variability of intertap intervals reflected the hierarchical organization. Intervals of the hypothesized leading hand were more stable than intervals of the non-leading hand. In the right-gallop, the right hand was more stable, whereas in the left-gallop the left hand was more stable. Also in line with the model's predictions, the correlational pattern of adjacent between-hand intervals indicate that the timing of the non-leading hand was more dependent on the timing of the leading hand than vice versa.

However, our results did not fully support the model presented in Figure 3.1. Firstly, we found no significant interaction between type of gallop and hand for the within-hand interval correlations. On the contrary, we found correlations close to 0 for each type of gallop and each hand. This indicates that the level of 'motor' variance is low relative to the 'clock' (or timekeeper) variance, in both hands. It is only in the presence of a relatively stable timekeeper, that motor variance will be characterized by a negative correlation between adjacent taps of each hand

(Turvey et al., 1989). In the anti-phase pattern, a (small) negative auto-correlation was found. Since there is no reason to expect a larger motor variance in the anti-phase than in the gallop, this is probably due to a lower timekeeper variance in anti-phase coordination. A possible explanation for the high timekeeper variance in the gallop is a feedback-based control mechanism. If the timekeeper is based on, or influenced by, feedback (proprioceptive, auditory and/or visual), then timekeeper variance is likely to be higher than motor variance.

Another important deviation from the model's predictions is the size of the correlations. Although we found a significant difference between the correlations of the two different pairs of adjacent between-hand interval (see Figure 3.2) in both the left- and the right-gallop, the difference was not as large as expected from the model. On the one hand, the model predicted strong negative correlations between RL-LR in the right-gallop, whereas values were only around -.30, a moderate correlation. These low values might be ascribed to the short interval (RL in the right-gallop and LR in the left-gallop) being more stable than the interval of the leading hand (RR in the right-gallop and LL in the left-gallop). On the other hand, the model predicted no correlation between LR and RL in the right-gallop, whereas we found a small, but distinctly negative correlation value. The equivalent holds true for the left-gallop. This inconsistency with the model's predictions suggests that the leading hand is also timed relative to the non-leading hand to some extent.

Furthermore, we did not find that the variability in each configuration of the gallop was related to the equation used for calculating the relative phase. This is in line with the suggestion made in the previous paragraph, that the effect of hand-role is not as strong as suggested by Figure 3.1. Relative phase variability is a relatively insensitive measure of hierarchical control compared to the interval variability and the correlations between adjacent intervals. Together, these results suggest that there is a leading and a non-leading hand, but that the contrast is not maximal.

In sum, the findings support the hypothesis that the gallop is hierarchically controlled, i.e., that different hand-roles are imposed upon the hands by the coordination pattern (type of gallop). In the right-gallop the right hand is leading, whereas in the left-gallop the left hand is leading. The timing of the leading hand is influenced by the timing of the non-leading hand, but this influence is smaller than the influence that the leading hand exerts on the non-leading hand. Figure 3.5 (panel A) shows the hierarchical model for the gallop, adapted according to

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the present findings. In multifrequency tasks, the different hand-roles are caused by the different tapping frequencies of the individual hands. The gallop, however, is defined in the phase relation between the hands. The hands perform the same movement at the same frequency, but with asymmetric time lags between them. Nevertheless, we found a hierarchical control mechanism, similar to the multifrequency studies. Thus, characteristics in the phase relation alone can lead to an asymmetric coupling of the hands that directly affects the differential stability between hands.

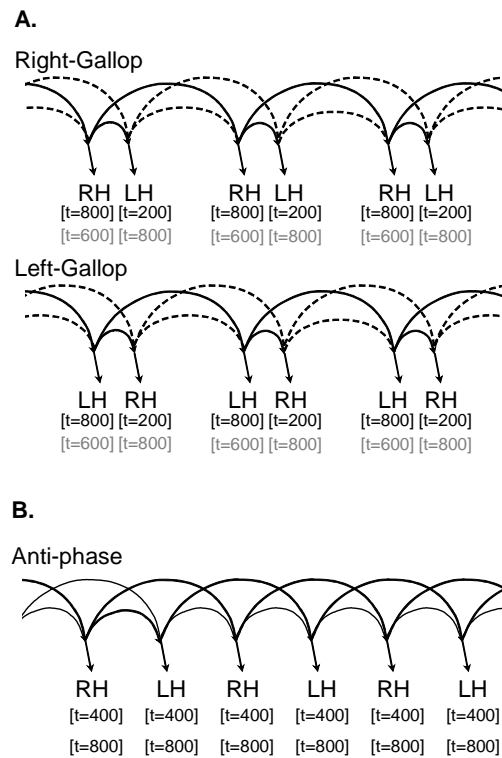**Figure 3.5 A** Hierarchical control model for the gallop, adapted from Figure 1 on the basis of the results. There is a leading hand, but not in the absolute sense as proposed in the first figure. **B** Symmetric control model for the anti-phase. There is no asymmetrical coupling and thus no leading hand. *RH* right hand, *LH* left hand.

The importance of hand-role in the gallop is further stressed by the finding that the phase shift was directly related to the type of gallop. The hypothesized leading hand (the left hand in the left-gallop and the right hand in the right-gallop) was slightly more than a quarter of a cycle ahead of the non-leading hand. In the literature, the source of a phase shift has been linked primarily to structural asymmetries of the body (for example, cerebral dominance; Stucchi & Viviani, 1993). Our results suggest that a phase shift can also have a functional origin. It could be that, for instance, 120°-phase difference is a stronger attractor than 90° and that the pattern is "pulled" toward the former coordination pattern. However, studies that have investigated the coordination stability of a wide range of coordination patterns in a bimanual tapping task found no stable attractors other than the in-phase and anti-phase patterns (Tuller & Kelso, 1989; Yamanishi et al., 1980). It has to be assumed that subjects were able to perform the 90°-phase pattern in the present study by establishing this attractor intentionally, guided by pacing (at the beginning of each trial) and instruction. An alternative explanation for the phase shift is that subjects positioned this intentional attractor slightly closer to the weaker of the two existing attractors, since the stronger attractor (i.e., the in-phase pattern) may have affected the stability of the new attractor to a greater extent. A final consideration is the perceptual meaning of the type of phase shift that we found. Although the phase patterns of the two configurations of the gallop are exactly opposite, they produce the same auditory feedback. In a tapping task, this auditory feedback may be an important part of the control mechanism. If so, one would expect that effects in one type of gallop are mirrored in the other. Apparently, this is the case for the intertap interval stability, the correlations and the phase shift. One would also predict that participants find it difficult to distinguish between the two gallop patterns. In fact, in a similar experiment with a group of elderly participants with and without Parkinson's disease, we observed frequent transitions between the left- and right-gallop. Moreover, the participants were often unaware of these transitions (Verheul & Geuze, 2001).

The second aim of the present study was to investigate whether the hand arrangement in the gallop was associated with a difference in coordination variability and/or intertap interval variability. No interaction between phase pattern and hand preference was found for both measures. This means that the gallop was performed equally proficiently in both hand arrangements. This cannot be explained by the low motor complexity of the tapping task, since hand

arrangement had a clear effect in multifrequency tapping (Peters, 1981). It may be concluded then, that the large effect of hand arrangement in multifrequency tasks is related to the asymmetry of frequency rather than the hierarchical coupling.

As mentioned above, the intertap-interval variability (averaged over the hands) did not differ significantly between the two types of the gallop. The variability of the preferred hand increased when it was not leading, but, in right-handers, the non-preferred hand became less variable. This means that the non-preferred hand can gain stability when the leading hand-role is imposed upon it by the definition of the task. This opens up possibilities for manipulating individual hand stability, which may be relevant in the functional rehabilitation of asymmetrically affected subjects, such as hemiplegic patients and patients with one-sided Parkinsonism.

In this study, we also tested two alternative models. The data did not support these. The first of model was a hierarchical model based on hand-preference instead of hand-role. None of the four predictions of the model was confirmed. Complex three-way interactions revealed two significant effects in the condition in which both hands were covered, but only one of these was in line with the model. The other effect pointed in the opposite direction. The symmetric coupling model, influenced by hand-preference, was not supported by our data either. Intertap interval variability of the hands was not related to hand-preference, and neither was the phase shift. Instead, the phase shift was found to be related to hand-role, providing additional support for the hierarchical coupling (hand-role) model.

3.4.2 *Anti-phase*

In contrast to the findings for the gallop, results for the anti-phase pattern point to a symmetric coupling between the limbs. All correlations (i.e., for within-hand and between-hand intertap intervals) were approximately similar. All were small, but distinctly negative. The timing of the left hand is as much dependent on the timing of the right as vice versa. Moreover, the dependency between the hands seems to be of the same strength as the dependency between the taps within one hand. These findings confirm that a symmetric coupling underlies anti-phase coordination (see Fig. 3.5, panel B).

In the present study, we did not replicate the effects of hand-preference that have been reported previously for the anti-phase pattern (Rogers et al., 1998;

Stucchi & Viviani, 1993; Treffner & Turvey, 1995). We did not find a difference in variability between the two hands and we found a phase shift that was much smaller than previously reported (for instance, Stucchi & Viviani (1993) reported that the asynchrony was about 25 ms with frequencies from 0.6 to 1.5 Hz.) and more importantly pointing to the non-preferred hand being slightly advanced instead of the preferred hand (the latter only significant in left-handers). The discrepancy between present and previous findings probably arises from task differences. The studies that produced a difference in variability between the hands focused on coordination tasks that were more complex than the tapping task we used. (for example, turning two wheels or drawing two circles). It is likely that hand-preference effects are more pronounced if the task is more complex. In relation to the phase shift, Stucchi and Viviani (1993) have argued that in a complex motor task, such as circle drawing, additional processing of the efferent commands is necessary to switch from the "default" option (i.e., in-phase) to anti-phase coordination. The order of activation of the muscles in one of the limbs has to be reversed in order to achieve an anti-phase pattern. They hypothesized that this extra processing occurs in the non-dominant cerebral hemisphere and results in an additional delay favoring a dominant hand lead. In the discrete, single-joint tapping task that we used, reversal of activation is not necessary. This may explain why our data did not show the large dominant hand lead in the anti-phase pattern reported by Stucchi and Viviani (1993) and Treffner and Turvey (1995).

A small phase shift like the one for the anti-phase pattern in the present study, could also be related to a difference in proficiency between the hemispheres with regard to the generation of the required limb movements. In a transcranial magnetic stimulation study (Triggs et al., 1994), hand-preference was shown to be related to the excitability of motor units. Also, a difference in stiffness between the limbs could cause systematic phase shifts in coordination (Bingham et al., 1991; Treffner & Turvey, 1995; Treffner & Turvey, 1996). Treffner and Turvey (1995) believed this "peripheral explanation" to be insufficient to account for the relatively large phase shifts reported in their study and the Stucchi and Viviani (1993) study. In our study, however, time lags were relatively short and this factor may thus have played a relatively larger role.

The direction of the phase shift, however, requires further explanation. The origin of the phase shift has been hypothesized to be related to an interhemispheric transfer delay or to attentional switching (Stucchi & Viviani,

1993; Treffner & Turvey, 1996). According to the first hypothesis, the phase shift is caused by a longer pathway from the lateralized "timekeeper" to the non-preferred hand (through the corpus callosum) than to the preferred hand. The second hypothesis suggests that information that is sent from the non-dominant to the dominant hemisphere arrives in an under-aroused, non-attentive hemisphere (Kinsbourne, 1970). The observed phase shift would be related to the time necessary for subcortical structures to arouse the relevant hemisphere. Both hypotheses are based on the idea of a dominant hemisphere for the rhythmical timing of the limbs. A classical study involving subjects with hemispheric lesions (Wyke, 1971) and a recent positron emission tomography study (Viviani et al., 1998) have delivered convincing evidence for this idea for in-phase coordination. It has been assumed that the phase shift in the anti-phase pattern is caused by the same mechanism (Stucchi & Viviani, 1993; Treffner & Turvey, 1995). However, no direct support has been presented as yet for this claim. Moreover, there are several indications that the anti-phase pattern is controlled in a different manner than the in-phase pattern. Studies with commissurotomy patients and congenital acallosal subjects show that anti-phase and more complex coordination patterns require interhemispheric activity (Jeeves et al., 1988; Preilowski, 1972), more so than in-phase coordination (Tuller & Kelso, 1989). Wing et al. (1989) have shown that a simple two-stage model of a single "timer" and two "motor" components cannot account for the variability in between-hand intervals during anti-phase tapping. A more complex model consisting of one timer with coupled motor delays of the two hands or a model of two coupled timers produced a qualitatively better fit to their data. How exactly this mechanism gives rise to a phase shift in the direction of the non-dominant hand remains a subject for future investigation.

3.4.3 *Attention*

The manipulation of attention had no main or two-way interaction effects on any of the variables studied. Three three-way interaction effects were found involving the allocation of attention. All effects indicated a significant interaction between hand-preference and another variable (equation, interval-pair, pattern) in the condition in which both hands were covered. This suggests that in this condition, the effect of hand-preference might be more pronounced than in other feedback conditions.

The inconsistent outcomes with respect to directing attention reported in the literature suggest that attentional manipulations are sensitive to their precise implementation. For instance, in the Amazeen et al. (1997) study, the subjects were instructed to swing two pendulums so that one pendulum oscillated between two targets situated over one of the hands and to tap the targets as lightly as possible to avoid overshooting. In the Swinnen et al. (1996) study subjects were instructed to trace the contours of two circles with two pens, while visually monitoring one of the hands. These two tasks require continuous coordination of the hands and a high level of visual guidance. The attentional effects reported in these studies may have resulted from the manipulations of visual feedback rather than attention. This is supported by the Stucchi and Viviani (1993) study, which reported no effect of the auditory manipulation of attention in a circle-drawing task. In the present study, attention was directed by manipulating visual feedback and instructing subjects before each trial to watch the visible hand(s). However, the individual movements (flexion and extension of the index fingers) did not require any visual guidance. In bimanual tapping, auditory and tactile feedback are probably the most dominant sources of information. Therefore, the manipulation of vision may have had little effect.

The hypothesis that hand-preference and hand-role are related to attention (Peters, 1994) does not have to be rejected on the basis of these findings. In all the attention studies, including ours, overt attention was manipulated. However, covert attention may play a far more important role. It is likely that hand-roles (such as leading and non-leading) are imposed upon the hands by an attentional mechanism. This is supported by the fact that the leading hand in the gallop is also perceived as leading (Banks & Prinzmetal, 1976; Bregman & Reidnicki, 1975).

4

Inter-limb Coupling in Bimanual Rhythmic Coordination in Parkinson's Disease

Abstract Recently, it has been shown that rhythmic inter-limb coordination is disturbed in patients with Parkinson's disease (PD). The present study aims to investigate whether this coordination deficit is primarily the result of an impaired coupling, related to hypoactivation of the supplementary motor area (SMA), or primarily the indirect result of an asymmetrical distribution of PD-symptoms over the left and right upper limb (a peripheral process). In order to do so, this study evaluates the performance of symmetrically and asymmetrically affected PD patients as well as the interaction of the asymmetric distribution of PD symptoms with task-induced asymmetries for stability of coordination and individual hand performance. Thirty PD patients and 30 matched control subjects tapped anti-phase and the left and right leading gallop patterns in four visual feedback conditions. Symmetrically affected subjects performed significantly worse than asymmetrically affected and control subjects in the gallop patterns. This result suggests that the central deficit has a stronger effect on inter-limb coupling in PD than the neuromuscular and biomechanical asymmetry between the limbs. However, the symmetrically affected subjects were significantly older than the asymmetrically affected subjects, which may have confounded the results. Detailed analysis of the asymmetrically affected subjects provided very little support for an explanation based on enhanced asymmetry, but do support the explanation based on the SMA deficit. The data suggest that this deficit may lead to a compensatory asymmetrical inter-limb coupling in the primarily right-affected patient group, and under specific circumstances also for the primarily left-affected patient group. The difference in coordination strategy between left- and right-affected patients suggests that pre-morbid hand-preference is an important structural constraint on the coupling strategies available to the subjects.

4.1 Introduction

Although there are other biochemical defects in Parkinson's disease (PD), research on clinical features of PD and their treatment suggests that a dopamine deficiency is the primary defect in PD (for an overview, see Sandler, 1977). The dopaminergic nigrostriatal neurons are progressively destroyed. As a consequence, basal ganglia functioning is seriously compromised (Marsden, 1982, 1984, 1990). Characteristic symptoms include rigidity, bradykinesia (moving slowly), hypokinesia (making slow and small movements) and akinesia (difficulty in movement initiation, "freezing"). Rest tremor is frequently observed. Recently, a growing body of evidence suggests that coordination between the upper limbs is also affected (Almeida et al., 2002; Byblow et al., 2000, 2002; Geuze, 2001; Johnson et al., 1998; Serrien et al., 2000a; Swinnen et al., 1997, 2000; Van den Berg et al., 2000).

The relative phase between the limbs is generally used as a measure of interlimb coordination (see, for example, Haken et al., 1985; Kelso et al., 1998). Relative phase variability during rhythmic in-phase (simultaneous) and anti-phase (alternating) interlimb coordination (such as bimanual finger tapping) was found to be increased in PD patients compared to healthy control subjects (e.g., Geuze, 2001; Johnson et al. 1998; Serrien et al., 2000a; van den Berg et al. 2000). Another way to assess the quality of coordination is to determine the critical frequency in an increasing frequency task. The critical frequency is the frequency at which subjects exhibit a spontaneous transition from the initial coordination pattern (usually anti-phase) to another, more stable, coordination pattern (usually in-phase). This critical frequency was found to be significantly lower in PD patients than in control subjects (e.g., Byblow et al. 2000, 2002; Geuze, 2001; Johnson et al. 1998). This combination of evidence indicates that coordination is less stable in PD patients than in healthy individuals of the same age.

It has been theorized that this coordination deficit in PD patients may be linked to a dysfunction of the supplementary motor area (SMA) (e.g., Johnson et al., 1998; Van den Berg et al, 2000). This mesial frontal cortical structure, located immediately anterior to the primary motor area, plays an important role in rhythmic bimanual coordination. Primate research has shown that anatomically, the SMA is bilaterally organized with strong projections of the hand representation through the corpus callosum to the SMA of the opposite hemisphere (Rouiller et al., 1994). Moreover, left and right SMA are usually

active together, even with unimanual movements (Roland et al., 1980). Neuroimaging studies have revealed that during bimanual anti-phase movements the SMA shows additional activation compared to unimanual and in-phase movements (Immisch et al., 2001; Sadato et al., 1997; Toyokura et al., 1999; Ullen et al., 2003). These studies looked at simple bimanual movement tasks, such as tapping with the index fingers (Ullen et al., 2003) and repetitive closing and opening of the fist (Toyokura et al., 1999). In line with these findings, transcranial magnetic stimulation (TMS) strongly affects anti-phase, but not in-phase, coordination in similar rhythmic coordination tasks (Meyer-Lindenberg et al., 2002; Serrien et al, 2002; Steyvers et al., 2003).

The SMA normally receives its major subcortical input, via the thalamus, from the basal ganglia (Cunnington et al., 1996; Williams et al., 2002). It is believed that in PD, the disruption of dopaminergic input to the striatum may indirectly impair the SMA. Indeed, PD patients show a reduction in cerebral blood flow in the SMA compared to control subjects (Kikuchi et al., 2001). It has often been suggested that less impaired cortical structures can show compensatory overactivity (e.g., Sabatini et al., 2000; Cunnington et al., 2001), although the evidence for such cortical reorganization is inconclusive (Buhmann et al., 2003). The most likely candidates to take on a compensatory function are the primary motor cortex and premotor cortex, areas that are reported to play a role in healthy rhythmic bimanual coordination (e.g., Debaere et al., 2001; Immisch et al., 2001; Lang et al., 1990; Toyokura et al., 1999), albeit secondary compared to the SMA. These structures are more unilaterally organized structures, compared to the SMA (Rouiller et al., 1994), especially when involved in distal upper limb movements (e.g., index finger tapping).

We hypothesize that inter-limb coordination with less involvement of the SMA and more involvement of the primary motor and premotor cortices will result in altered inter-limb coupling. In healthy individuals, cortical control of inter-limb coordination is not the summed activity for the control of each hand in combination with a "coupling factor" (e.g., Toyokura et al., 1999). However, it may resemble this type of control when cortical areas are involved that are less designed for tight, intricate central control of inter-limb coupling. For instance, it is likely that the coupling is more strongly dependent on sensory feedback loops. In line with this, it has been reported frequently in the literature that in PD patients, coordination relies more heavily on conscious control and external

guidance than in healthy individuals of the same age (e.g., Oliviera et al., 1998; Verschueren et al., 1997).

In sum, inter-limb coupling appears to be compromised at a central level in PD patients. In bilaterally affected PD patients, coordination difficulty during anti-phase coordination and more complex coordination tasks would be a direct result of this impairment. In individuals that are asymmetrically affected by Parkinson's disease, inter-limb coupling is also likely to be impaired. Unilateral lesion of the SMA in macaque monkeys has been shown to affect bimanual coordination (Brinkman, 1984). In hemiparkinsonism, however, a compensatory asymmetrical coupling strategy between the two limbs may be observed in rhythmic coordination tasks. In a bimanual tapping task, this would result in a hierarchical control mechanism: the affected side produces a series of taps and the relatively unaffected side interlaces its taps in such a manner that the required coordination pattern arises (Fig. 4.1). Although the affected side is "leading" the movement, the relatively unaffected side actually effectuates the required coordination pattern. This distribution of hand-roles is more likely than the reverse, since the reproduction of movement frequency remains largely intact in PD patients whereas the relative phasing (the control of the phase lag) is affected (Ventre-Dominey et al., 2002). One could compare this uni-directional coupling to the case in which an individual coordinates its movements with an external rhythmic signal so that a specified coordination pattern arises. This type of coordination is inherently less stable than a bi-directional coupling mechanism (Byblow et al., 1995).
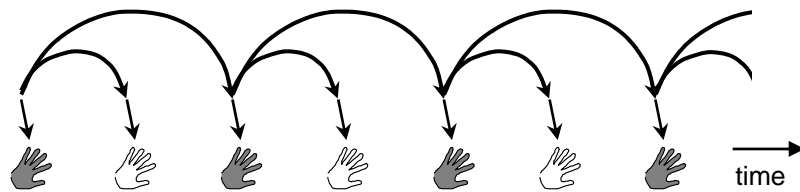

Figure 4.1 The hierarchical coupling model as an extreme form of altered inter-limb coupling. The affected hand (dark) is tapping more or less regularly and the relatively unaffected hand (light) is strategically interlacing its taps, so that the required coordination pattern (in this case anti-phase) arises.

PD symptoms such as rigidity and tremor are often asymmetrically distributed over the lateral sides of the patient, i.e., one side of the body may be more severely affected by the disease than the other side. It can be argued that it is not the impaired inter-limb coupling that is the primary cause of the coordination deficit, but rather the biomechanical asymmetry between the limbs that is enhanced and subsequently affects coordination negatively. The proportion of asymmetrically affected patients is especially large in mildly to moderately affected patients, exactly the group for which the bimanual coordination deficit has been established. A large number of studies of normal subjects has focused on the effects of asymmetric oscillators on interlimb coordination (e.g., Fuchs et al., 1996; Jeka & Kelso, 1995; Kelso & Jeka, 1992; Peck & Turvey, 1997; Rosenblum & Turvey, 1988; Sternad et al., 1999; Treffner & Turvey, 1995). In most of these studies, individuals were asked to swing two pendulums with a different eigenfrequency in a symmetrical (i.e., in-phase), alternating (i.e., anti-phase) or "galloping" (i.e., 90° out of phase) coordination mode. Relative phase variability increased when the asymmetry between the oscillators (e.g., the difference in eigenfrequency) increased (e.g., Peck & Turvey, 1997; Rosenblum & Turvey, 1988). Inducing a difference in stiffness between the wrists was shown to change the phase relation between the limbs (Bingham et al., 1991). Similarly, the asymmetric distribution of symptoms in PD may cause instability of interlimb coordination. A small study including four PD patients indeed suggested that asymmetrical tremor induced "symmetry breaking", i.e., a de-stabilization of coordination dynamics (Van Emmerik & Wagenaar, 1995).

The present study aims to investigate whether the impaired coupling or the enhanced asymmetry is primarily responsible for the coordination deficit in PD. It aims to distinguish between the two possible underlying mechanisms by testing several contrasting predictions of the two proposed models in a bimanual tapping task. Firstly, the quality of coordination in asymmetrically affected patients will be compared to the quality of coordination in symmetrically affected patients. According to the enhanced limb asymmetry hypothesis, the asymmetrically affected patients should perform worse. The impaired coupling hypothesis, however, predicts the opposite effect. As mentioned above, according to this hypothesis the asymmetrically affected subjects have the possibility of a hierarchical control mechanism, in which the relatively unaffected side compensates for the instability of the affected side. The movements of the relatively unaffected side can be timed in relation to the movements of the

affected side so that the required coordination pattern arises. Such an alternative control mechanism is not available to the symmetrically affected patients. In these subjects, the coupling is assumed to be disturbed in both directions. It has to be noted that since the disease tends to progress from one-sided to bilateral (and all symptoms gradually become worse) a simple comparison between symmetrically and asymmetrically affected patients would not suffice. If the symmetrically affected subjects would show a more stable coordination than the asymmetrically affected subjects this would strongly suggest that the enhanced asymmetry hypothesis is correct. However, if the reverse is found, it cannot be concluded yet that the hierarchical coupling hypothesis must be true.

Pre-morbid right-handed subjects form the largest group of patients and therefore they are the focus of this study. The enhanced asymmetry hypothesis predicts that the primarily left-affected patients will be performing worse than the primarily right-affected group, since the disease strengthens the pre-morbid asymmetry (i.e., hand-preference) in the former group and decreases asymmetry in the latter. In contrast, if bimanual coordination in asymmetrically affected PD subjects is based on a one-directional coupling, coordination is expected to be most successful when the right hand is relatively unaffected, i.e., in left-affected patients. The right hand, being the pre-morbid preferred hand, would be more proficient at accurately interlacing the beats in between the beats of the preferred hand to create the desired pattern.

Three further contrasting predictions will be tested for the asymetrically affected patients in particular. Firstly, the two proposed models make specific predictions about the relative stability of individual hand movements underlying coordination. According to the enhanced asymmetry hypothesis, the movements of the affected hand will be less stable than the movements of the relatively unaffected hand as a direct result of the asymmetric distribution of symptoms. The hierarchical coupling hypothesis however predicts that the affected hand will be equally stable as or more stable than the relatively unaffected hand. Taps of the relatively unaffected hand are interlaced in the intervals of the taps of the affected hand so that the required coordination pattern arises. As a consequence, variability of tapping with the relatively unaffected hand is equal to or higher than variability of the affected hand.

Secondly, a hierarchical control can be revealed by the analysis of the correlation between adjacent inter-tap intervals (Summers et al., 1993). Following the control model shown in Figure 4.1, variations in the timing of the non-

affected hand will not influence the taps of the affected hand. However, variations in the timing of the affected hand will influence the timing of the unaffected hand. In other words, the between-hand intervals between two taps of the affected hand will be negatively correlated (Fig. 4.2). No such correlation would exist between the two intervals between two taps of the relatively unaffected hand. The asymmetry hypothesis predicts no systematic correlation between adjacent intertap intervals.
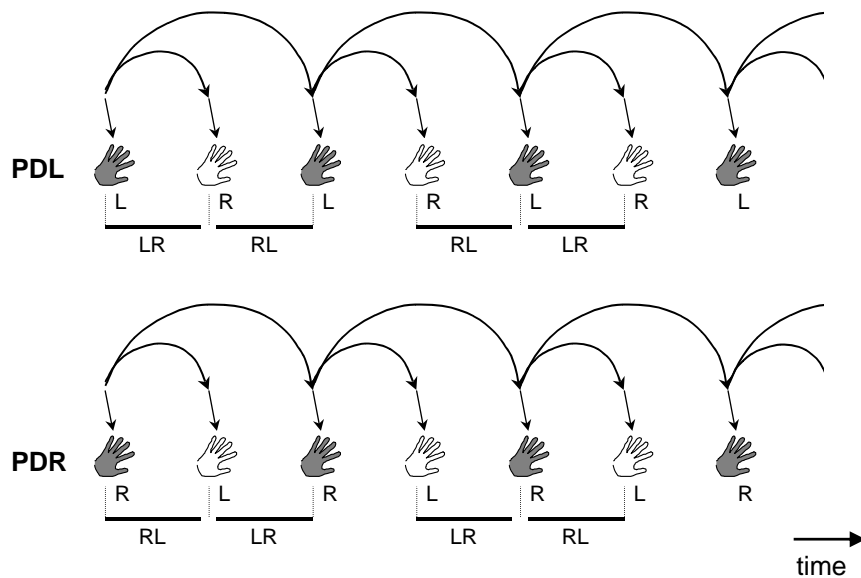
Figure 4.2 The effect of group on the correlation between inter-tap intervals, predicted by the hierarchical control model. Fluctuations in the timing of the most affected hand (dark) have a direct influence on the timing of the relative unaffected hand, but the reverse is not the case. Consequently, if the interval between a tap of the affected hand and the subsequent tap of the unaffected hand (depicted at the far left in the time-series) lengthens, then the subsequent interval to the next tap of the affected hand shortens, and vice versa. This would be revealed by a negative correlation between the two intervals. No such correlation is predicted for the two intervals between two taps of the relatively unaffected hand (depicted on the right in the time series).

Finally, asymmetry (hand-preference, differential loading of the limbs, etc.) in healthy individuals is associated with a phase shift (Stucchi & Viviani, 1993; Swinnen et al., 1996; Treffner & Turvey, 1995, 1996). The preferred hand tends to be slightly "ahead" of its required position or timing, causing a small shift in the relative phase. The phase shift increases when the preferred hand is swinging a pendulum of a higher eigenfrequency than the pendulum swung by the non-preferred hand (Treffner & Turvey, 1996). The phase shift also becomes larger when the intrinsic asymmetry is further enhanced by explicitly focusing visual attention on the preferred hand (Amazeen et al., 1997; Swinnen et al., 1996). Thus, the additive effects of present asymmetries determine the phase shift. The intrinsic functional asymmetry between the two sides of the body is enhanced when the non-preferred side is more affected by PD than the preferred side. This is the case in the left-affected patients in this study. For the right-affected patients, the two asymmetries are opposite in direction. Assuming that the relatively unaffected side has functionally become the preferred side in these patients, the resultant asymmetry would be in the opposite direction as for the left-affected patients. In line with this evidence, the enhanced asymmetry hypothesis predicts a phase shift associated with the relatively unaffected hand being slightly advanced and/or the affected hand lagging behind slightly. However, the phase shift has been shown to be related to handedness only in non-hierarchical (symmetrical) coupling structures. In hierarchically controlled coordination, the phase shift appears to be related to the leading hand-role, regardless of hand arrangement (and thus hand-preference) (Verheul & Geuze, 2003). Hence, the hierarchical coupling hypothesis predicts the hierarchically superior hand to be slightly advanced relative to the subordinate hand.

It has been argued (Peters, 1994) that the effects of intrinsic asymmetry become particularly apparent when the hands are required to perform an asymmetric task. In this experiment, two task-induced asymmetries will be studied: the gallop pattern, and the asymmetric allocation of attention induced by the manipulation of visual feedback and instruction.

The iso-frequency gallop is a well-known asymmetric coordination pattern, defined by a relative phase of 90° (e.g., Fontaine et al., 1997; Peck & Turvey, 1997). There are two types of the gallop pattern: the left-gallop (the left hand is a quarter of a cycle ahead of the right hand) and the right-gallop (the right hand is a quarter of a cycle ahead of the left hand). In healthy individuals, the gallop has been shown to impose a hierarchical distribution of hand-roles (i.e., leading and

interlacing) on the hands (Verheul and Geuze, 2003). The hand that taps a quarter of a cycle ahead of the other hand normally fulfills the leading hand-role. If the coordination deficit in PD arises from enhanced asymmetry, it is expected that coordination is more stable when the hand on the relatively unaffected side takes on the leading hand-role and the hand at the affected side is hierarchically coupled to it than vice versa. This means that primarily left-affected patients will perform the right-gallop more stable than the left-gallop whereas primarily right-affected patients will perform the left-gallop more stable than the right-gallop. The hierarchical coupling hypothesis on the other hand suggests that successful coordination will arise in asymmetrically affected patients when the hierarchical coupling due to the disease matches the hierarchical coupling imposed upon the hands by the asymmetric gallop pattern. In the reverse, conflicting, situation, coordination is expected to be particularly impaired.

The second task-induced asymmetry in this experiment is the allocation of attention induced by the manipulation of visual feedback so that only one of the hands can be seen combined with the instruction to look carefully at the visible hand. Many studies on Parkinson's disease have emphasized the dependence on conscious control and external cues in PD patients. Motor performance in PD shows similarities with unlearned motor behaviour (Morris & Iansek, 1996). The movements are correct, i.e., the muscles that are used and their order of activation appear to be functional, but performance is unstable and slow (Marsden, 1982). PD patients have particular difficulty with two simple motor tasks at the same time (Schwab et al., 1959). They show similarly impaired behaviour in a single task as healthy subjects in a double task (task combined with Stroop task) (Brown & Marsden, 1991). This suggests that the automaticity of movements is particularly impaired and that patients rely heavily on conscious control and external guidance. Providing external guidance has been shown to improve performance more than in healthy subjects (Kritikos et al., 1995; Jahanshahi, 1992; Jones et al., 1992). PD patients can learn new motor tasks, but they remain strongly dependent on external information when performing the learned tasks (Verschueren et al., 1997). A PET imaging study by Samuel et al. (1997) has shown that during a complex finger movement sequence, PD patients can switch to using circuits normally involved in facilitating cued movement, i.e., the lateral premotor and inferolateral parietal regions. Rehabilitation of PD patients is often directed at developing conscious control or learning to use external guidance by focussing on components of movements, visualizing and reciting words when

writing, using visual clues (walking on lines on the floor etc.) or thinking about the goal of the movement in relation to an imaginary stimulus (Morris & Iansek, 1996). In sum, PD patients more strongly rely on visual guidance and conscious control than healthy adults.

In sharp contrast to the extensive knowledge on the effects of (removal of) visual feedback for PD patients, there are no studies on the effects of *asymmetrical* feedback. The asymmetrical allocation of attention might, however, have a large effect on coordination stability and may be informative as to the nature of the impairment. Removing feedback from one hand and forcing attention on the other hand will be effective when this is in concordance with the normal functional asymmetry between the hands, but disruptive when this is in conflict. According to the enhanced asymmetry model, directing attention to the non-affected hand would be beneficial to coordination stability, similar to the effect found in healthy adults when focusing on the preferred hand in bimanual coordination tasks like circle-drawing and pendulum swinging (Amazeen et al. 1997; Swinnen et al., 1996). In these studies, the increase in stability was accompanied by an increase in phase shift. When focusing on the non-preferred hand, the reverse was found. The impaired coupling hypothesis does not make a prediction about attention. It cannot be deduced from the model whether coordination would benefit from directing attention to the "leading" hand (the "timer") or to the hand that interlaces taps to create the required coordination pattern. Findings from this study may elucidate this issue.

The previous arguments are largely derived from research in healthy young adults. Since PD patients are mostly elderly individuals, interpretation of results is hindered by the confounding effect of age. Therefore, we have included a control group, matched with respect to age and gender to the PD group. For this group, we expect coordination dynamics to be similar to the dynamics in young adults as reported in Verheul and Geuze (2003), i.e., we expect (i) the anti-phase pattern to be more stable and more accurate than the gallop patterns, and the gallop patterns to be equally stable and accurate; (ii) the preferred hand to be more stable than the non-preferred hand in the anti-phase, and the leading hand to be more stable than the lagging hand in the gallop patterns; (iii) the preferred hand to be advanced in the anti-phase, and the leading hand to be advanced in the gallop, as indicated by phase shifts; (iv) equally small negative correlations for RL-LR and LR-RL for the anti-phase, and stronger negative correlations particularly for RL-LR in the

right-gallop, and for LR-RL in the left-gallop (Fig. 4.2); (v) attention to have no effect or a small, modulating effect.

4.2 Methods

4.2.1 *Subjects*

The experiment was approved by the Ethics Board of the Academic Hospital Groningen. The subjects were 30 patients with mild Parkinsonism and 30 control subjects. All subjects gave their written informed consent prior to participation. The patient group consisted of outpatients of the neurological polyclinic of the Academic Hospital Groningen and the Martini Hospital Groningen, who volunteered to participate after being informed about the experiment by their neurologist. Inclusion criteria were the diagnosis of idiopathic Parkinson's disease, Hoehn & Yahr stage 1.0 to 2.5 (i.e., mild PD; Hoehn & Yahr, 1967), a positive response to medication (if medicated), and pre-morbid right-handedness. Exclusion criteria were the presence of other neurological or motor disorders than PD, dementia, and the use of antidepressants and neuroleptics. Individual data for each PD patient are given in Table 4.1. Patients were on their regular PD-medication during the experiment. The control group consisted of partners of the patients and volunteers from the community. Exclusion criteria were the presence of neurological or motor disorders, dementia, and the use of antidepressants and neuroleptics. Age was matched ± 4 years, on average the age of a patient differed 1.4 years from the age of its control subject. The average age of the PD group was 64.8 years (range 37-89) and the average age of the control group 65.0 years (range 35-87).

All subjects completed a hand-preference questionnaire (Van Strien 1992; Van Strien and Bouma, 2000; Appendix I). The PD patients were asked to report their pre-morbid hand-preference. The questionnaire is based on the most reliable and valid items from several handedness questionnaires (Annett 1970; Oldfield 1971; Raczkowski et al. 1974). On this questionnaire –10 denotes extreme left-handedness and +10 extreme right-handedness. All subjects scored +8 or higher, most scored +10.

Table 4.1 Clinical details of the PD subjects.

Most affected side	Age (yrs)	Sex	Disease duration (yrs)	UPDRS-on total (right/left)	Medication*
Left	37	F	8.7	24 (3/14)	P
Left	42	M	4.6	18 (5/10)	P, Sy
Left	58	M	14.8	8 (1/5)	M, Sy, R
Left	59	M	5.1	16 (4/6)	Si, A
Left	60	M	11.2	13 (2/4)	M
Left	62	F	10.1	17 (2/10)	P
Left	64	F	2.5	22 (4/10)	No medication
Left	66	M	6.8	26 (6/10)	M
Left	73	F	9.6	16 (2/6)	M, P
Left	73	F	8.6	25 (6/11)	Sy, M
Right	50	F	3.1	9 (7/10)	P
Right	55	M	6.4	28 (11/7)	M, R
Right	56	M	9.5	11 (3/1)	R, E
Right	57	F	0.6	11 (6/2)	No medication
Right	58	F	2.1	21 (8/3)	No medication
Right	68	M	17.3	23 (10/6)	Si, P, A
Right	69	F	11.1	32 (18/7)	Si
Right	70	M	3.2	29 (11/7)	Si
Right	72	M	1.2	22(8/5)	No medication
Right	72	M	2.7	15 (5/2)	Si
Both	52	M	10.7	24 (9/10)	Si, P, E
Both	64	F	8.5	14 (5/6)	E, Si
Both	68	M	14.8	14 (5/4)	Si, R, Se
Both	71	F	0.7	17 (7/7)	No medication
Both	72	M	7.5	24 (8/7)	M
Both	74	M	5.6	22 (6/8)	Si
Both	76	F	17.8	16 (7/6)	M, Sy, E
Both	77	F	1.3	12 (3/4)	No medication
Both	81	M	3.9	16 (5/4)	Si
Both	89	F	0.5	24 (6/5)	Si

Note. *Sinemet® (Si) contains levodopa with carbidopa, Madopar® (M) contains levodopa with benserazide. Permax® (P) and Requip® (R) contain pergolide and ropinirol, respectively (levodopa agonists). Artane® (A) contains trihexyfenidyl (anti-cholinergic). Symmetrel® (Sy) contains amantadine (aspecific synaps stimulator). Eldepryl® (E) and Selegiline® (Se) both contain selegiline (MAO-B-inhibitor).

Since depression in PD patients is not uncommmon (Meara et al., 1999), all subjects (including the control subjects) were asked to fill out a translated version of the 15-item Geriatric Depression Scale (Sheikh & Yesavage, 1986; translated version Kok, 1994; Appendix II). This scale is particularly suitable for elderly and PD subjects, since it includes less questions referring to symptoms that could be due to a diminished physical health than other depression scales. 2 PD subjects scored 7 (possible scoring range 0-15), indicating mild depression. All other subjects scored between 0 and 5, which indicated they were not depressed.

For patients, in most cases, the experiment was combined with the patient's regular visit to the Hospital. Unified Parkinson's Disease Rating Scale (UPDRS) motor scores were collected from the patients (on medication) directly prior or after the experiment by qualified neurologists, usually the subject's own neurologist. The UPDRS rating scale (Fahn and Elton, 1987) is a reliable and valid instrument for evaluating PD symptoms (Martinez-Martin et al., 1994). The motor part of the UPDRS partly consists of items that evaluate each side of the body separately. This is the case for tremor at rest, action tremor, rigidity, finger taps, hand grips, hand pronate/supinate and leg agility (Appendix III). If the total score of these items for one body side was 1.5 times or more the score for the other side, the subject was classified as asymmetrically affected. Scores for speech, facial expression, posture, etc. were taken into account for calculating the total score, but not in calculating whether the subject was asymmetrically affected. In this manner, three subgroups were defined: a symmetrically affected, a primarily left-affected and a primarily right-affected subgroup. Details of the subgroups are given in Table 4.2. The symmetrically affected subgroup was significantly older than the primarily left-affected subgroup. No other significant differences were found for the variables in this table.

Table 4.2 Composition of the three PD subgroups.

	Mostly left affected	Mostly right affected	Symmetrically affected
N	10	10	10
Gender	5F / 5M	4F / 6M	5F / 5M
Age (yrs)	59 (11.8)	63 (8.3)	72* (10.0)
UPDRS	18.6 (6.0)	20 (8.2)	18.1 (4.4)
Duration (yrs)	8.2 (3.6)	5.7 (5.4)	7.1 (6.0)

Note. Standard deviation between brackets. *Main effect age $F_{(2,27)}=4.47$, p<.05. Tukey HSD post-hoc test: Mostly left affected v. symmetrically affected p<.05.

4.2.2 *Apparatus*

Two touch-sensitive buttons (diameter 2.5 cm, 7.5 cm apart) that were built into the slanted surface of a box (30 x 20 x 2 to 6 cm) were used to register finger taps. The fingers produced a slight sound when they touched the buttons. The box also served as a support for the hands. Visual feedback was manipulated by an adjustable black plate that was situated above the hands, but did not restrict their movements. During the first 6 cycles of each trial, a PC generated acoustic pacing signals (beeps lasting 75 ms) for both hands, specifying a phasing of 90° (gallop) or 180° (anti-phase) between the hands. The frequency of initial pacing was 1.25 Hz for each finger.

4.2.3 *Procedure*

Subjects were seated in a comfortable chair at a table. Their hands rested on the box. Their index fingers rested on the buttons. Subjects were asked to tap with their index fingers on the buttons, while their arms, hands and remaining fingers rested on the box and table surface throughout each trial. They were instructed to tap one of the coordination patterns at the frequency paced for the first six cycles as constantly as possible, and to continue tapping after the pacing stopped until the signal to stop was given by the experimenter. Three patterns were tapped: anti-phase, 90°-phase difference with the left hand leading and 90°-phase difference with the right hand leading. Before the beginning of each trial, the experimenter told the subject which pattern to tap and reminded him/her to watch the visible hand or hands carefully. Each pattern was tapped once in each of four visual feedback conditions: no feedback, left hand feedback, right hand feedback and full feedback from both hands. The four feedback conditions were randomized over subjects, and the patterns were randomized within those feedback conditions. This resulted in a total of 12 bimanual tapping trials per subject. The experimenter demonstrated each pattern. One practice trial for each pattern was given with full visual feedback. All trials lasted 21 cycles.

4.2.4 *Data reduction*

Only the self-paced parts of the trials were analyzed. The parameter describing coordination is the relative phase (ϕ), calculated as follows:

$$\phi = (L_n - R_n)/(R_{n+1} - R_n) \times 360° \tag{1}$$

in which L and R are the points in time at which the left and right index finger hit a button. In previous research, no significant difference was found when using this equation for the calculation of the relative phase compared to a similar equation that has the left-hand interval as denominator (Verheul & Geuze, 2003). Sign inversion for the left-gallop lead to both the left- and right-gallop being indicated by a relative phase of 90°.

To assess general task performance, we first analyzed whether subjects were able to maintain the required coordination pattern throughout the trial. If the average relative phase of the trial was not the required relative phase ± 45°, the trial was marked as unsuccessful. When a left-gallop was required but subjects tapped a right leading gallop or vice versa (a common observation), this mistake was not counted as a failed trial. The trial was then repeated. Only if subjects repeatedly tapped one type of gallop throughout the experiment, even after additional instruction, were these counted as failures.

To assess coordination stability, the standard deviation of the relative phase during constant, self-paced tapping was calculated. The phase shift was calculated as the deviation from the required relative phase in each trial. To assess accuracy, the absolute value of the phase shift, i.e., the absolute error, was analyzed. Furthermore, inter-tap interval (ITI) variability was calculated for each hand as the standard deviation of the inter-tap intervals of that hand. Finally, the correlation between adjacent inter-tap intervals was calculated (Fig. 4.2). For each trial, the average correlation was determined for all the intervals between two consecutive taps of the right hand (intervals RL and LR), and for all the intervals between two consecutive taps of the left hand (intervals LR and RL).

4.2.5 *Statistical analysis*
A multi-stage sampling design was employed, i.e., multiple measurements within multiple subjects. Due to the non-normality of the data (as indicated by Shapiro-Wilks tests), non-parametric tests had to be used. The Friedman analysis of variance by ranks and the Wilcoxon signed-rank test were used for within-group (between-condition) comparisons, i.e., comparisons relating to the effects of phase pattern, visual attention, hand and interval pair. Because each PD subject had been matched with a control subject, the Wilcoxon test was also used to compare the PD subgroups with the matched control subgroup. To compare the three PD subgroups, the Kruskal-Wallis test was used. Since statistical comparisons involving the symmetrically affected subgroup were limited to the

anti-phase condition (see Results, paragraph 1), we performed a separate analysis (using the Mann-Whitney *U*-test) to compare the left- and right-affected PD-groups in all conditions. The significance level α was set at .05. Post-hoc pair-wise comparisons for the Friedman and Kruskal-Wallis tests (Siegel & Castellan, 1988) were performed where necessary.

4.3 Results

This section is structured as follows. Since subjects frequently failed to perform the task successfully, we present data on general task performance first. Next, we will present the results for each group separately (within-group effects), before comparing the groups (between-group effects). First, the main effects of group (for between-group comparisons) will be presented, then the main effects of phase pattern and the effects of group in specific phase patterns. Next, the factors of hand (for inter-tap interval variability) and interval-pair (for correlation) are considered in addition to group and phase pattern. Finally, effects in specific attentional conditions (in general or in specific phase patterns) are considered. Median scores are presented in the text. Since the symmetrically affected PD group performed extremely poorly in the gallop patterns, the results and comparisons related to this group will only be based on performance in the anti-phase pattern.

4.3.1 Task Performance

Table 4.3 summarizes task performance in both PD patients and control subjects. Often, subjects failed to perform the required pattern in a stable manner throughout the trial. Nine out of the thirty control subjects failed in one or more trials, but only four out of those nine failed in two or more of the twelve trials. All control subjects were able to tap the anti-phase pattern correctly, but several were unable to perform one or both of the gallop patterns. Most often, the average relative phase value over the trial fell within the boundaries of the anti-phase instead of the required gallop pattern (patterns were defined ± 45°). In a minority of the trials, phase wandering or a transition occurred. In general, control subjects failed more often on the left-gallop than on the right-gallop.

Table 4.3 Task performance per group.

	Anti-phase subjects	trials	Left-gallop subjects	trials	Right-gallop subjects	trials
Control (*n*=30)	0	0	8 (27)	19 (16)	4 (13)	9 (8)
PD Symm (*n*=10)	<u>1 (10)</u>	4 (10)	**<u>7 (70)</u>**	**<u>23 (58)</u>**	**6 (60)**	**17 (43)**
PD Asymm (*n*=20)	**6 (30)**	15 (19)	<u>6 (30)</u>	<u>16 (20)</u>	**12 (60)**	**27 (34)**
PD Right (*n*=10)	**4 (40)**	**10 (25)**	3 (30)	7 (18)	**5 (50)**	**12 (30)**
PD Left (*n*=10)	2 (20)	5 (13)	3 (30)	9 (23)	**7 (70)**	**15 (38)**

Note. Number of subjects per group failing to perform a specific coordination pattern in at least one trial, and the total number of failed trials in these subjects (total number of trials per pattern = 4). In brackets the equivalent as a percentage of total number of subjects or trials, respectively. In bold particularly high incidence in PD compared to matched control group. Underlined indicates large difference between the PD group that is symmetrically affected and PD group that is asymmetrically affected. PD Symm = bilaterally symmetrically affected PD patients; PD Asymm = asymmetrically affected PD patients, further divided into a primarily right-affected (PD Right) and a left-affected (PD Left) subgroup.

Seven PD-patients failed to perform a stable anti-phase pattern in one or more anti-phase trials (controls never failed in this pattern). In the failed trials, they tapped the left-gallop, the right-gallop or a 2:1 rhythm (i.e., one of the hands tapping twice as fast as the other). As a group, the bilaterally affected patients performed better than the asymmetrically affected patient groups, with the right-affected patients performing the worst.

Difficulty in tapping the gallop patterns was far more common in PD patients than in controls. Whereas nine controls failed in at least one of the eight gallop trials, this number was 20 for the PD patients (7 primarily left-affected, 5 primarily right-affected and 8 bilaterally symmetrically affected patients). If a criterion of two fails is used, then 4 controls performed insufficiently (13%) versus 16 PD patients (53%). Subjects repeatedly tapped the anti-phase pattern, a 2:1 rhythm, or (in one of the left-affected PD subjects) an in-phase pattern instead of a gallop.

In sum, the PD subjects differed from the control subjects in the amount of failed trials. The bilaterally symmetrically affected PD patients failed more often than controls in the left- and right-gallop patterns. The asymmetrically affected PD patients failed more often than controls in the right-gallop and in the anti-phase pattern, with right-affected patients failing twice as often in the anti-phase pattern as left-affected patients. Overall, the highest incidence of failure, both between and within subjects, was found in the symmetrically affected PD-group (Fig. 4.3). Since in four of the ten bilaterally affected patients performance in the gallop was so poor that statistical analysis of the coordination stability and accuracy was impossible (i.e., three of them failed in all eight gallop trials, and one in seven), this group was excluded from further analysis of the gallop patterns. In the PDL and PDR groups, subjects failed in some trials, but rarely consistently in all trials in a specific pattern.
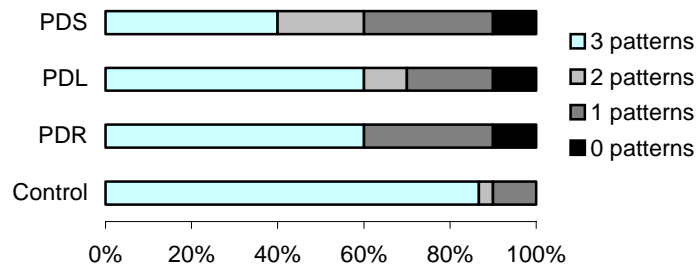
Figure 4.3 Success in performing the task. For each group, the proportion of subjects is given that is successful at performing 0, 1, 2 or 3 (i.e., all) patterns, when a criterion of 50% (2 trials) is used for success in each pattern.

4.3.2 Within-group effects

4.3.2.1 *Control subjects*

4.3.2.1.1 *Phase pattern*

A summary of results for the control subjects is shown in Table 4.4. A main effect of phase pattern was found for coordination stability and accuracy within the control group (stability $\chi^2_{(2)} =18.47$, $p<.001$; accuracy $\chi^2_{(2)} =45.60$, $p<.001$). Pair-wise comparisons showed that coordination in the control subjects was

significantly more stable and more accurate in the anti-phase pattern than in the left- and the right-gallop patterns (stability: $p<.01$, $p<.05$ respectively; accuracy: both $p<.001$). A further effect of pattern was found for phase shift ($\chi^2_{(2)} = 36.87$, $p<.001$). A small negative phase shift was found in the anti-phase pattern, indicating the left hand was slightly advanced, compared to large phase shifts in the gallop patterns. The large negative phase shift in the left-gallop indicated that subjects tapped too fast with the left hand and/or too slow with the right hand, whereas the large positive phase shift in the right-gallop indicated the reverse. In both cases, this led to the relative phase shifting approximately 20° away from the gallop pattern in the direction of the anti-phase pattern. Pair-wise comparisons showed that the phase shifts in all three patterns were significantly different from each other (anti-phase - left-gallop $p<.05$; anti-phase - right-gallop $p<.01$; left-gallop - right-gallop $p<.001$).

Table 4.4 Performance of the control subjects.

	Anti-phase	Left-gallop	Right-gallop
Relative phase variability (°)	7.3_a (6.4; 10.3)	10.8_b (7.3; 15.0)	9.8_b (7.5; 13.9)
Absolute error (°)	3.0_a (2.1; 4.2)	20.3_b (9.9; 31.5)	17.5_b (8.9; 28.1)
Phase shift (°)	-0.3_b (-1.8; 0.6)	-19.4_a (-31.5;-4.6)	17.5_c (6.2; 28.1)
Inter-tap interval variability (ms)	27.7_a (23.0; 34.4)	37.9_b (27.3;53.0)	32.6 (27.1; 43.7)
Left hand (ms)	28.0_a (22.6; 32.6)	36.8_b (27.9; 54.8)	30.8 (26.9; 46.8)
Right hand (ms)	27.4_a (23.3; 34.1)	38.8_b (25.7; 54.8)	33.1 (26.2; 41.8)
Correlation RL-LR	-.16 (-.27; -.04)	-.24 (-.37; -.16)	-.33 (-.50; -.06)
Correlation LR-RL	-.17 (-.31; .01)	-.25 (-.38; -.00)	-.26 (-.44; -.08)

Note. Median scores. Between-subject variability between brackets (25th and 75th percentiles). Medians in the same row with different subscripts differ at p<.05, for example the absolute error in the anti-phase pattern differed significantly from the absolute error in the two gallop patterns.

A main effect of phase pattern was also found for inter-tap interval variability ($\chi^2_{(2)}$ =16.07, $p<.001$). Similar to the variability of the relative phase, the variability of inter-tap intervals was lower in the anti-phase pattern than in the left- and right-gallop. The inter-tap intervals were more stable in the right-gallop than in the left-gallop. Pair-wise comparisons revealed that only the difference in variability between the anti-phase and the left-gallop was significant ($p<.001$). The main effect of phase pattern for the correlation between intervals RL and LR just failed to reach significance ($p=.072$). No effect of phase pattern was found for the correlation between LR and RL.

4.3.2.1.2 *Hand and interval-pair*

For both hands, an effect of phase pattern was found for inter-tap interval variability (left $\chi^2_{(2)}$ =17.1, $p<.001$; right $\chi^2_{(2)}$ =19.3, $p<.001$). Pair-wise comparisons revealed that both hands tapped significantly more variable in the left-gallop than in the anti-phase pattern (both $p<.001$). Inter-tap-interval variability did not differ significantly between the left and right hand. Neither was a main effect found of interval-pair (RL-LR and LR-RL) for correlation. Also, no effects of hand or interval-pair were found in specific phase patterns.

4.3.2.1.3 *Attention*

The manipulation of attention had no effect on coordination stability and phase shift in the control subjects. In contrast, a main effect of attention was found for accuracy ($\chi^2_{(3)}$ =7.96, $p<.05$). Accuracy was lower in the asymmetrical than in the symmetrical attention conditions in all three phase patterns. Pair-wise comparisons showed a significant difference between the left-hand-covered and the both-hands-covered conditions (absolute error left covered 17.0°; both covered 12.5°; $p<.05$). No other main effects of attention were found.

In the left-gallop (Fig. 4.4A) a comparison of inter-tap interval variability of the left and right hand indicated that the right hand tapped significantly more stable than the left hand, when the left hand was covered and attention was directed to the right ($z=-1.92$, $p<.05$). In line with these findings, the correlation between subsequent intervals RL and LR was significantly stronger than the correlation between intervals LR and RL in the same condition (Fig. 4.4A, $z=-2.44$, $p<.01$). The interval-pair RL-LR showed the strongest correlation in this attention condition (-0.34) compared to the other attention conditions, whereas the
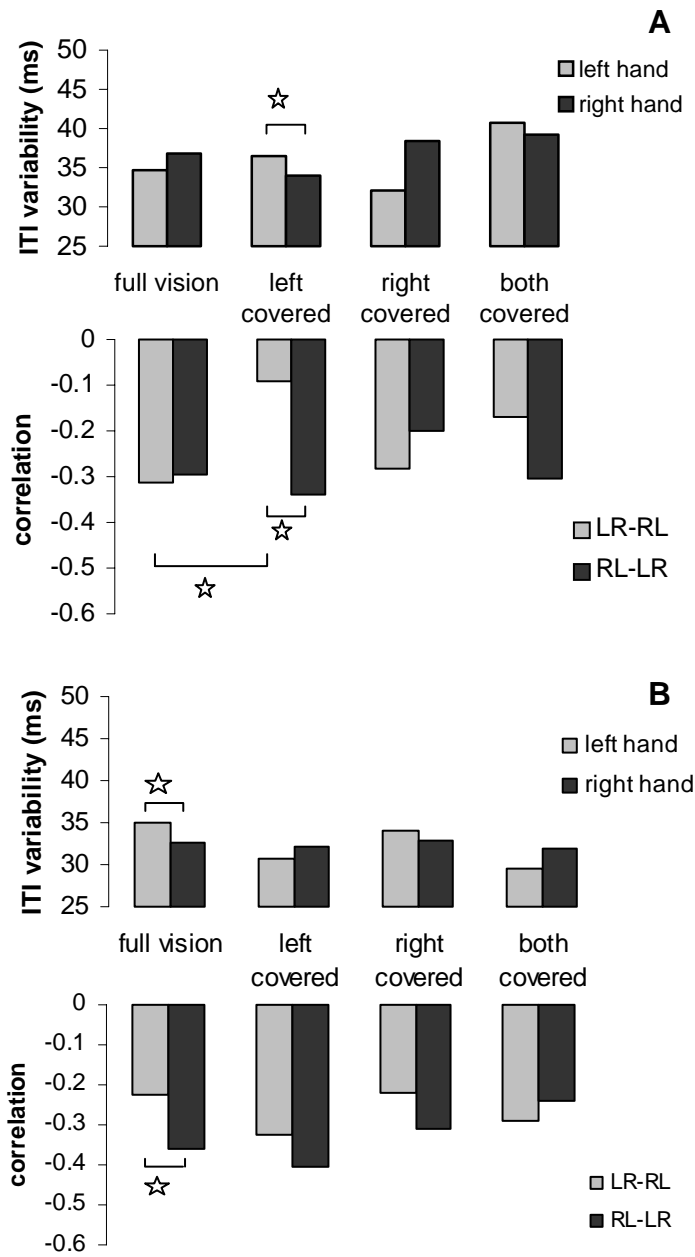
Figure 4.4 Behavior of the control group in the left-gallop (A) and right-gallop (B). Stars indicate significant differences between conditions.

interval-pair LR-RL showed the weakest correlation in this condition (-0.09). A significant effect of attention was found for the correlation between LR and RL in the left-gallop pattern ($\chi^2_{(3)}$ =8.80, *p*<.05). Pair-wise comparisons revealed that the correlation was significantly weaker when the left hand was covered than when both hands were visible (Fig. 4.4A; *p*<.05).

In the right-gallop (Fig. 4.4B) the right hand was significantly more stable than the left hand when both hands were visible (*z*=-1.99; *p*<.05). Comparison of the two types of correlation revealed that the RL-LR correlation was significantly stronger than the LR-RL correlation in this condition (*z*=-1.99; *p*<.05).

In sum, as can be seen in Figure 4.4, findings point to an asymmetrical coupling with the right hand leading when the left hand was covered in the left-gallop and when both hands were visible in the right-gallop.

4.3.2.2 *Asymmetrically affected PD subjects*

4.3.2.2.1 *Phase pattern*

Tables 4.5 and 4.6 show results for the primarily left-affected patient group (PDL) and the primarily right-affected patient group (PDR), respectively. The difference in coordination stability between the patterns was not significant for the PD groups (*p*=.06 for both groups; in the control group it was significant at p<.01). Similar to the control subjects, however, phase pattern had an effect on accuracy ($\chi^2_{(2)}$ =7.80, *p*<.05 for both groups). Pair-wise comparisons indicated that both groups were significantly less accurate in the right-gallop than in the anti-phase pattern (both *p*<.05). Also similar to the control subjects, an effect of phase pattern was found for phase shift (PDL $\chi^2_{(2)}$ =7.8, *p*<.05; PDR $\chi^2_{(2)}$ =11.4, *p*<.01). Like the controls, the PD subjects showed an almost negligible phase shift in the anti-phase, and large negative and positive phase shifts in the left- and right-gallop, respectively. Pair-wise comparisons revealed for both PD groups that the phase shifts in the gallop patterns were significantly different (PDL *p*<.05; PDR *p*<.01).

The variability of inter-tap intervals was higher in the gallop patterns than in the anti-phase pattern. The left-affected patients showed lower inter-tap interval variability in the left-gallop than in the right-gallop, whereas the right-affected patents showed lower inter-tap interval variability in the right-gallop than in the left-gallop, similar to the control subjects. A main effect of pattern was found for each group (PDL $\chi^2_{(2)}$ =11.4, *p*<.01; PDR $\chi^2_{(2)}$ =6.2, *p*<.05). Pair-wise comparisons showed that for the PDL group the difference in inter-tap interval

variability between the anti-phase and the right-gallop was significant ($p<.01$), and that for the PDR group the difference between the anti-phase and left-gallop was significant ($p<.05$).

Table 4.5 Performance of the primarily left-affected PD group (PDL).

	Anti-phase	Left-gallop	Right-gallop
Relative phase variability (°)	**11.1** (9.1; 12.3)	13.2 (10.6; 13.9)	**14.3** (11.1; 18.0)
Absolute error (°)	**11.5**$_a$ (5.8; 16.1)	19.5 (14.2; 29.2)	<u>**34.5**</u>$_b$ (17.2; 39.9)
Phase shift (°)	-1.6 (-8.9; 11.4)	-17.2$_a$ (-29.1;-9.9)	30.2$_b$ (0.1; 38.4)
Inter-tap interval variability (ms)	**35.3**$_a$ (29.7; 44.7)	39.4 (34.9; 44.2)	**41.4**$_b$ (35.4; 51.6)
Left hand (ms)	**34.5** (31.7; 46.3)	37.4 (32.0; 44.1)	**42.1** (36.7; 48.3)
Right hand (ms)	38.0 (28.2; 41.8)	40.4 (32.8; 46.8)	40.0 (34.3; 55.8)
Correlation RL-LR	-.28 (-.46; -.09)	-.28 (-.40; -.19)	-.27 (-.44; -.07)
Correlation LR-RL	-.17 (-.44; .10)	-.30 (-.46; -.21)	-.25 (-.38; .01)

Note. Median scores. Between-subject variability between brackets (25th and 75th percentiles). Medians in the same row with different subscripts differ significantly. Bold: significantly different from control subjects. Underlined: significantly different from PDR group.

4.3.2.2.2 *Hand and interval-pair*

The effect of pattern just failed to reach significance (p=.06) in the left and right hand individually for the PDL group. In the PDR group, both hands tapped significantly more variable in the left-gallop pattern than in the anti-phase pattern (left $\chi^2_{(2)}=7.2$, $p<.05$; right $\chi^2_{(2)}=7.4$, $p<.05$; post-hoc both p<.05).

Furthermore, a main effect of hand was found for the PDR group. The right hand was significantly more stable than the left ($z = -2.40$, $p<.01$). The medians were similar (right 36.0; left 36.9), but the 75th percentile values were clearly different (right 47.2; left 55.7). Since no effect of hand was found in the control subjects, this indicates a compensatory role for the left hand in the PDR group, i.e., asymmetrical coupling strategy in which the affected hand (right hand) is

leading and the left hand is interlacing taps. No effect for interval-pair was found to support this. In the PDL group no difference in stability between the hands was found. No other effects were found for inter-tap-interval variability and correlation, without considering attentional conditions.

Table 4.6 Performance of the primarily right-affected PD group (PDR).

	Anti-phase	Left-gallop	Right-gallop
Relative phase variability (°)	**10.1** (6.8; 11.7)	14.3 (8.0; 17.8)	13.6 (8.8; 15.4)
Absolute error (°)	**6.2**$_a$ (3.5; 12.5)	17.9 (8.0; 30.9)	<u>18.0</u>$_b$ (10.3; 25.0)
Phase shift (°)	0.1 (-3.5; 6.3)	-17.7$_a$ (-30.9;-3.3)	18.0$_b$ (8.8; 25.0)
Inter-tap interval variability (ms)	**28.9**$_a$ (25.1; 47.4)	39.8$_b$ (28.3; 59.5)	39.2 (34.5; 45.8)
Left hand (ms)	**30.8**$_a$ (25.8; 45.1)	43.7$_b$ (26.6; 71.5)	41.6 (29.6; 47.2)
Right hand (ms)	**29.6**$_a$ (24.0; 45.9)	36.5$_b$ (30.0; 46.8)	**39.8** (32.8; 44.2)
Correlation RL-LR	-.28 (-.46; -.00)	-.34 (-.47; -.26)	-.37 (-.52; -.19)
Correlation LR-RL	-.24 (-.31; -.08)	-.25 (-.48; -.04)	-.28 (-.36; -.11)

Note. Median scores. Between-subject variability between brackets (25th and 75th percentiles). Medians in the same row with different subscripts differ significantly. Bold: significantly different from control subjects. Underlined: significantly different from PDL group.

4.3.2.2.3 *Attention*

For the PDR group, main effects of attention were found for the difference in inter-tap interval variability between the hands, and the difference in correlation between the two interval-pairs (inter-tap-interval (ITI) variability $\chi^2_{(3)}$ =10.8, *p*<.05; correlation $\chi^2_{(3)}$ =8.4, *p*<.05). Pair-wise comparisons revealed that in both cases, the measurements in the two asymmetrical attention condition (left hand covered, right hand covered) differed significantly (both p<.05). When the left hand was covered, the right hand was more stable than the left (ITI variability right 36.2 ms; left 40.1 ms), and the correlation RL-LR was stronger than LR-RL (RL-LR -.37; LR-RL -.18). The opposite was the case when the right hand was

covered, although differences were smaller (ITI variability right 35.5 ms; left 32.5 ms; correlation RL-LR -.19; LR-RL -.26). No main effects of attention were found for the PDL group.

The above pattern of results for ITI variability and interval correlation for the PDR group could be identified within the anti-phase and left-gallop patterns, but not in the right-gallop (no significant effect in the latter). When the left hand was covered in the anti-phase condition, the right hand tapped significantly more stable than the left hand (ITI variability right 29.2 ms; left 32.6 ms; z=-1.89, p<.05) and the correlation between RL and LR was significantly stronger than the LR-RL correlation (RL-LR -.27; LR-RL -.13; z=-1.79, p<.05). When the left hand was covered in the left-gallop, the right hand was also significantly more stable than the left (z=-1.78, p<.05). The latter is shown in Fig. 4.5A. Thus, in the anti-phase and left-gallop, the PDR group showed an asymmetrical coupling with the right hand leading (i.e., a compensatory coupling) when the left hand was covered.

For the PDL group (Fig. 4.6A), the opposite was found in the latter condition (left hand covered in left-gallop), viz. the left hand was significantly more stable than the right (z =-1.89, p<.05). Within the left-gallop, a significant effect of attention was also found for coordination stability within the PDL group ($\chi^2_{(3)}$ =12.4, p<.01). Pair-wise comparisons showed that coordination was significantly more variable when the left hand was covered and attention was consequently directed to the right, than when both hands were covered (relative phase variability 14.1° and 10.7°, respectively; p<.05). Thus, the PDL data point to an asymmetrical coupling with the left hand leading when the left hand was covered in the left-gallop, but no effect for correlation was found to support this. This finding coincides with low coordination stability.

For the PDR group, an effect of attention was found for phase shift in the right-gallop ($\chi^2_{(3)}$ =9.00, p<.05), indicating that the phase shift was significantly smaller when both hands were covered than when both hands were visible (covered 5.4°; visible 20.0°, p<.05). No other effects of attention were found.

Figure 4.5 Behavior of the PDR group in the left-gallop (A) and right-gallop (B). Open star indicates significant difference between conditions. Gray and black stars indicate significant difference with control and PDL group, respectively.

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Figure 4.6 Behavior of the PDL group in the left-gallop (A) and right-gallop (B). Open star indicates significant difference between conditions. Gray and black stars indicate significant difference with control and PDR group, respectively.
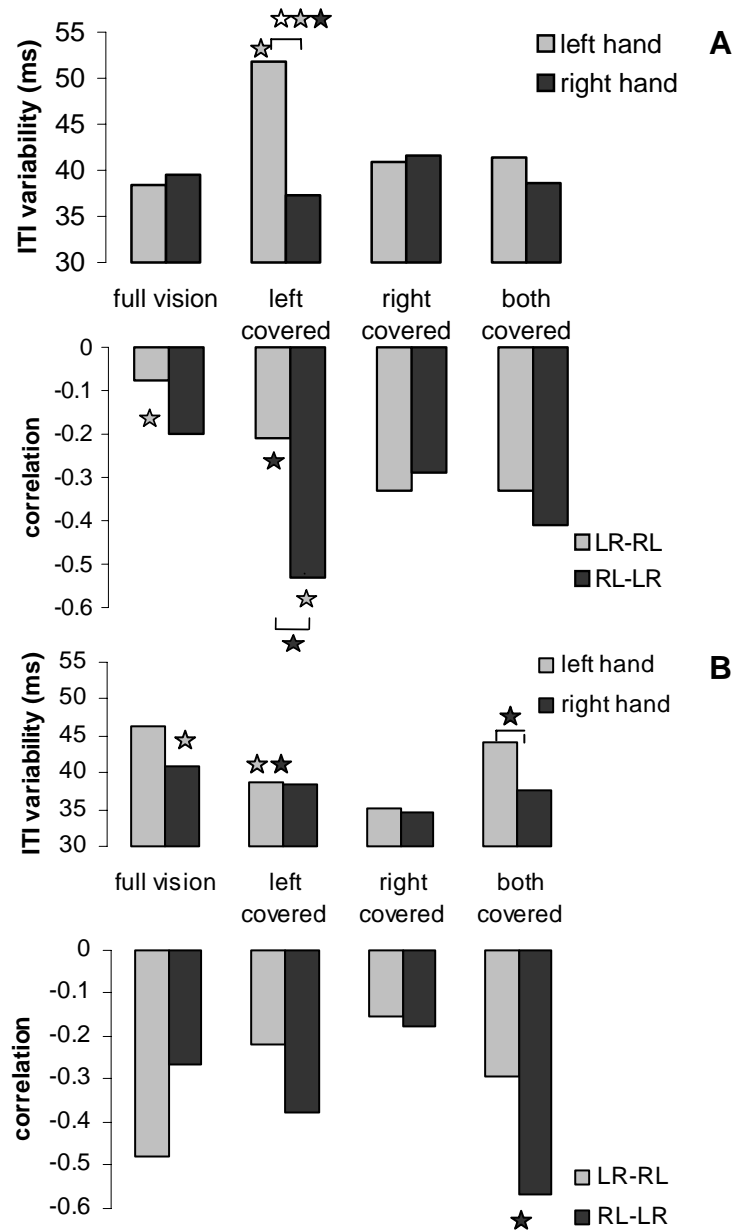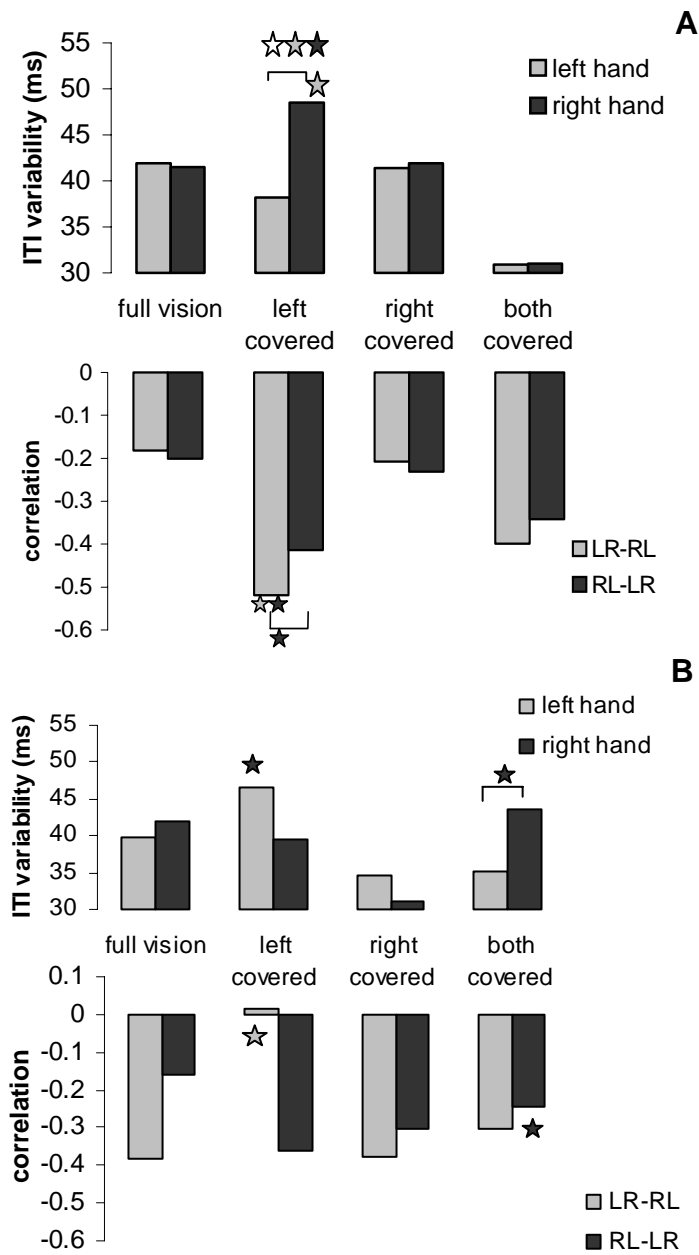
4.3.2.3. *Bilaterally symmetrically affected group (anti-phase only)*
Performance of the symmetrically affected PD group in the anti-phase is summarized in Table 4.7.

Table 4.7 Performance of the bilaterally symmetrically affected PD group in the anti-phase coordination pattern.

	Anti-phase
Relative phase variability (°)	12.2 (9.8; 16.2)
Absolute error (°)	8.7 (3.5; 10.8)
Phase shift (°)	-5.4 (-9.6; 1.6)
Inter-tap interval variability (ms)	**39.8** (29.6; 43.9)
Left hand (ms)	**38.4** (33.2; 46.7)
Right hand (ms)	**36.9** (27.4; 44.2)
Correlation RL-LR	-.34 (-.49; -.05)
Correlation LR-RL	-.10 (-.26; -.01)

Note. Median scores. Between-subject variability between brackets (25th and 75th percentiles). Bold: significantly different from control subjects.

4.3.2.3.1 *Hand and interval-pair*
No main effects were found for hand or interval-pair.

4.3.2.3.2 *Attention*
Figure 4.7 shows the inter-tap interval variability of the hands and the correlation values for adjacent interval pairs RL-LR and LR-RL in all attention conditions in the anti-phase pattern. Attention had an effect on the inter-tap interval variability of the left hand ($\chi^2_{(3)}$ =8.76, *p*<.05) and the correlation between LR and RL ($\chi^2_{(3)}$ =8.76, *p*<.05). Pair-wise comparisons showed that the inter-tap intervals of the left hand were significantly more stable when both hands were visible (32.1 ms) than when the left hand was covered (46.7 ms). In line with this, the correlation between LR-RL was significantly stronger when both hands were visible (-.41) than when the left hand was covered (.04). For both effects *p*<.05.

Furthermore, the right hand was significantly more stable than the left when both hands were covered (ITI variability right 39.7 ms; left 46.3 ms, z=-2.70, p<.01), and the correlation between RL and LR was significantly stronger than the correlation between LR and RL in this condition (RL-LR -.32; LR-RL .04, z=-2.50, p<.05). Thus, an asymmetrical coupling was found with the right hand leading when both hands were covered in the anti-phase.

Combining the results for attention, it appears that when the left hand is not visible (i.e., in the left hand covered and the both hands covered conditions), its tapping intervals become highly irregular, and the right hand takes on the leading hand-role. The reverse is not the case.
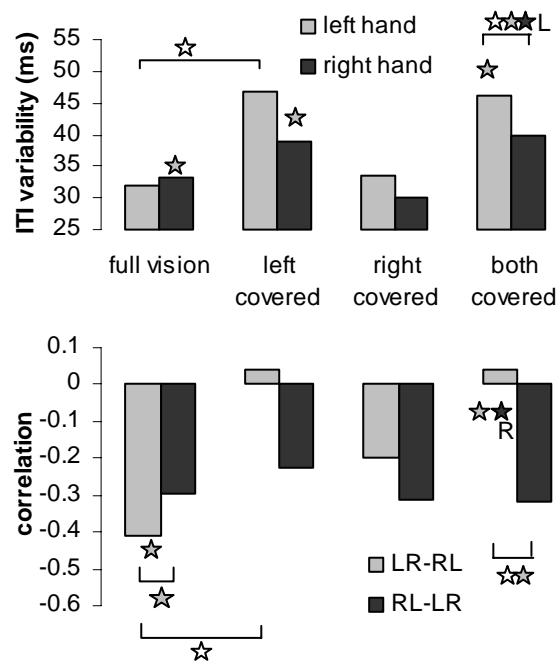

Figure 4.7 Behavior of the symmetrically affected PD group (PDS) in the <u>anti-phase</u> pattern. Open star indicates significant difference between conditions. Gray star indicates significant difference with control subjects. Black star indicates significant difference with PDL (L) or PDR (R) group.

4.3.3 Between-group comparisons
4.3.3.1 *Asymmetrically affected PD subjects versus control subjects*
4.3.3.1.1 *Group*
Both asymmetric PD groups showed more variable coordination throughout the experiment than their matched control subjects (PDL z=-2.09, p<.05; PDR z=-2.19, p<.05). Coordination in the PDL group was also less accurate than in the control group (z=-1.78, p<.05). Inter-tap interval variability was higher in both PD groups compared to the controls throughout the experiment (PDL z=-1.99, p<.05; PDR z=-2.29, p<.05). See also Tables 4.4, 4.5 and 4.6 (note that Table 4.4 contains percentile data for all controls; the tests were run with a subset of the controls, i.e., the matched subjects only).

4.3.3.1.2 *Phase pattern*
In the anti-phase condition, the differences between the controls and the PD groups were most striking (again, see Tables 4.4, 4.5 and 4.6). In this condition, the control subjects performed better than both PD groups in terms of coordination stability (PDL z=-1.99, p<.05; PDR z=-2.29, p<.05), accuracy (PDL z=-2.50, p<.01; PDR z=-2.50, p<.01) and inter-tap interval variability (PDL z=-1.68, p<.05; PDR z=-2.50, p<.01). In the right gallop, coordination in the PDL group was significantly less stable (z=-1.89, p<.05) and less accurate (z=-1.99, p<.05) than in the control subjects and inter-tap intervals were more variable (z=-1.78, p<.05). No further differences were found between the asymmetrically affected PD subjects and the controls relating to phase pattern.

4.3.3.1.3 *Hand and interval-pair*
Notably, the PDL group showed a more variable performance with the left hand compared to their matched control subjects (main effect group z=-2.19, p<.05), whereas the PDR group was more variable with both hands (left z=-2.19, p<.05; right z=-2.40, p<.01).). This supports the idea of a compensatory hand-role for the left hand in the PDR group, noted in paragraph 2.2.2. Within the anti-phase pattern, the same pattern of results was found (PDL left z=-2.19, p<.05; PDR left z=-2.19, p<.05; PDR right z=-2.70, p<.01). In the right-gallop, the PDL group tapped significantly more variable with the left hand than control subjects (z=-2.19, p<.05), whereas the PDR group tapped significantly more variable with the

right hand compared to controls (z=-2.09, p<.05). In the left-gallop, no effect of group was found for either hand.

The PDL group showed a significantly larger difference between the two types of correlation than controls in the anti-phase pattern (z=-1.68, p<.05). Whereas controls showed similar correlations for the two interval-pairs in the anti-phase pattern, the PDL group showed a substantially stronger correlation between RL and LR than between LR and RL (see Tables 4.4 and 4.5), suggesting an asymmetrical coupling with the right hand leading (i.e., opposite to a compensatory coupling), but this was not supported by results for inter-tap interval variability of the two hands.

4.3.3.1.4 *Attention*
Significant differences for coordination stability between the PD groups and the controls were found in the condition in which the right hand was covered for the PDL group (PDL: 13.4°; Control for PDL (CL) 9.1°; z=-2.09, p<.05), and in the condition in which the left hand was covered for the PDR group (PDR: 12.7°; Control for PDR (CR) 7.5°; z=-2.40, p<.01). The PDR group also showed a significantly different phase shift than the controls when the left hand was covered (PDR 3.7°; CR: -1.6°) and when both hands were visible (PDR 4.3°; CR -3.7°). When the left hand was covered, the strongest effect for inter-tap interval variability was found for both groups (PDL and PDR: 39.0 ms; CL 30.8 ms; CR 29.5 ms; PDL z=-2.19, p<.05; PDR z=-2.50, p<.01). The PDL group showed a stronger correlation between RL and LR than controls in the right-hand covered condition (PDL -.31; CL -.12; z=-1.78, p<.05), whereas the PDR group showed a stronger correlation when both hands were covered (PDR -.44; CR -.18; z=-1.78, p<.05).

In the left-gallop, both groups differed significantly from the control subjects with respect to several variables in the condition in which the left hand was covered (indicated by gray stars in Fig. 4.5A and 4.6A for ITI and correlation results). First, coordination in both groups was significantly less stable than in the controls (PDL 14.1°; CL 10.0°; PDR 14.5°; CR 9.3°; PDL z=-1.68, p<.05, PDR z=-2.29, p<.05). Secondly, the difference in inter-tap interval variability between the left and right hand was significantly larger in both PD groups than in the control group (PDL z=-2.09, p<.05, PDR z=-1.99, p<.05). Whereas the hands were approximately equally stable in the controls, there was a strong right-hand lead in the PDR group (Fig. 4.5A) and a left-hand lead in the PDL group (Fig.

4.6A). This was also reflected by the finding that the left hand was significantly more variable in the PDR group than in the controls ($z=-1.78$, $p<.05$), and the right hand was significantly more variable in the PDL group than in the controls ($z=-1.78$, $p<.05$). Thirdly and in concordance with the previous results, the correlation between RL and LR was significantly stronger in the PDR group than in the controls ($z=-1.99$, $p<.05$), whereas the correlation between LR and RL was significantly stronger in the PDL group ($z=-1.89$, $p<.05$). This combination of results strongly suggests that both left- and right-affected PD subject showed a compensatory asymmetrical coupling, and that this coupling is significantly more asymmetrical than the asymmetrical coupling found for controls in this condition.

When both hands were visible in the left-gallop, the correlation between LR and RL was significantly weaker in PDR than in control subjects (Fig. 4.5A; $z=-1.99$, $p<.05$). No other effects were found within the left-gallop.

In the right-gallop, the correlation between LR and RL was significantly weaker in the PDL group than in controls when the left hand was covered (Fig. 4.6B; $z=-1.99$, $p<.05$). When both hands were covered, coordination in the PDR group was significantly less stable but more accurate than in the control subjects (stability PDR 12.9°; CR 7.2°; $z=-1.78$, $p<.05$, accuracy PDR 6.8°; CR 19.0°; $z=-2.60$, $p<.01$). When both hands were visible, the inter-tap interval variability was significantly higher in the PDR group than in the controls (PDR 42.5 ms; CR 34.4 ms; $z=-1.99$, $p<.05$), specifically for the right hand (Fig. 4.5B; $z=-2.80$, $p<.01$). Finally, the left hand was significantly less stable in the PDR group than in the controls when the left hand was covered and attention was directed to the right (Fig. 4.5B; $z=-1.68$, $p<.05$). The latter finding supports the compensatory role of the left hand (the relatively unaffected hand) in the PDR group in this condition (see paragraph 2.2.3).

4.3.3.2 *Symmetrically affected PD subjects versus Control subjects (anti-phase)*
4.3.3.2.1 *Group*
No main effects of group were found for coordination stability, accuracy or phase shift. Inter-tap interval variability was significantly higher in the symmetrically affected PD subjects (PDS) than in their matched controls (CB) in the anti-phase pattern (PDS 39.8; CB 28.8; $z=-2.19$, $p<.05$). This does not imply that coordination in PDS subjects was more stable than in PDL and PDR subjects (for whom significant differences with control subjects were found), because control groups differ for the various PD subgroups. Since the PDS group was

significantly older than the other two PD groups, the same applies of course to the age-matched control group. In fact, relative phase variability is higher in the PDS group than in the PDL and PDR group (25th, 50th and 75th percentile, see Tables 4.5, 4.6 and 4.7).

4.3.3.2.2 *Hand and interval-pair*

The symmetrically affected PD subjects tapped significantly more variable with both hands than controls (PDS left 45.1; right 42.7; CB left 44.1; right 41.0; left *z*=-2.09, *p*<.05; right *z*=-2.09, *p*<.05). No interaction was found between group and hand or between group and interval-pair.

4.3.3.2.3 *Attention*

Accuracy was higher in all conditions in the symmetrically affected PD subjects (PDS) than in control subjects, but this difference was only significant in the condition in which the right hand was covered (PDS 10.8°, CB 2.3°; *z*=-2.09, *p*<.05). The phase shift was also significantly larger in the PDS group (8.1°) than in the controls (1.4°) in this condition (*z*=-1.99, *p*<.05).

The effects for inter-tap interval variability and correlation are given in Figure 4.7. Most group effects were found for the condition in which both hands were covered. In this condition, the PDS subjects tapped significantly more variable with the left hand than their control subjects (CB 28.5 ms; *z*=-2.40, *p*<.01). Inter-tap interval variability in general (regardless of hand) was also significantly more variable in the PDS group (43.3 ms) than in controls (30.5 ms) (*z*=-1.99, *p*<.05). Furthermore, the correlation between LR and RL was significantly weaker in the PDS subjects than in the control subjects (CB -.38; *z*=-1.89, *p*<.05). The difference between left and right hand inter-tap interval variability was significantly larger in the PDS subjects than in control subjects (*z*=-2.80, *p*<.01). In line with this, the difference in correlation between the two interval-pairs was also much larger in the PDS subjects than in controls (*z*=-2.70, *p*<.01). These results all confirm an asymmetrical coupling with the right hand leading in this condition in the PDS group, as suggested in paragraph 2.3.2.

When the hands were both visible, PDS subjects tapped more variable with the right hand than control subjects (CB 27 ms; *z*=-2.09, *p*<.05). Also, the correlation between LR and RL was significantly stronger in PDS subjects than in controls (CB .01; *z*=-2.29, *p*<.05). The difference in correlation between the two interval-pairs was also significantly larger in PDS subjects than in controls (*z*=-1.99,

p<.05). This suggests the left hand may have been leading when both hands were visible.

Finally, when the left hand was covered, PDS subjects tapped significantly more variable with the right hand than control subjects (CB 26.9 ms; *z*=-2.70, *p*<.01) and the inter-tap interval variability, regardless of hand, was also considerably higher in PDS subjects (42.7 ms) than in controls (26.0 ms) (*z*=-2.09, *p*<.05). No further effects were found.

4.3.3.3 Symmetrically versus asymmetrically affected PD subjects (anti-phase)
4.3.3.3.1 *Group*

No main effects were found for group.

4.3.3.3.2 *Hand and interval-pair*
No main effects were found for hand or interval-pair. Also, no interactions were found between hand or interval-pair and group.

4.3.3.3.3 *Attention*
Significant effects were only found in the condition in which both hands were covered and as a consequence no visual feedback was available from the hands. There was a group effect for the difference between the left and right hand inter-tap interval variability ($\chi^2_{(2)}$=7.00; *p*<.05) and for the correlation between LR and RL ($\chi^2_{(2)}$=6.68; *p*<.05). Pairwise comparisons showed that the difference in ITI variability between the left and right hand was significantly larger in the symmetrically affected PD subjects than in the PDL subjects (PDL left 34.5, right 32.7; PDS left 46.3, right 39.7). This provides further support for an asymmetrical coupling in this condition in the PDS group, already noted in paragraphs 2.3.2 and 3.2.3. Secondly, the correlation between LR and RL was significantly weaker in the symmetrically affected PD subjects than in the PDR group (PDS .04; PDR -.20). For both effects p<.05.

4.3.3.4 Left-affected versus right-affected PD subjects
4.3.3.4.1 *Group*

Comparing the two patient groups, no main effect of affected side was found for any of the dependent variables. The main effect for accuracy just failed to reach significance (*p*=.06).

4.3.3.4.2 *Phase pattern*

Accuracy was significantly lower in the PDL group than in the PDR group in the right-gallop (See Tables 4.5 and 4.6; z=-2.04, $p<.05$). Further significant differences were found in specific attention conditions.

4.3.3.4.3 *Hand and interval-pair*

No significant main effects were found for hand or interval-pair. Also, no significant interactions were found between hand or interval-pair and phase pattern and/or group.

4.3.3.4.4 *Attention*

When the right hand was covered, the PDR group was more accurate than the PDL group (PDR 16.1°; PDL 25.7°; z=-2.34, $p<.01$). The PDR group was also more accurate when both hands were covered in the right-gallop (Fig. 4.5B and 4.6B; z=-2.73, $p<.01$). In that same condition, the PDR group also showed a significantly smaller phase shift than the PDL group (PDR 5.4°; PDL 25.2°; z=-2.12, $p<.05$). When the left hand was covered, anti-phase coordination was significantly more stable in the PDR than the PDL group (PDR 8.5°; PDL 11.2°; z=-1.82, $p<.05$).

The difference in inter-tap interval variability between the left and right hand was significantly different for the two asymmetrically affected PD groups when the left hand was covered and when both hands were covered (left z=-1.81, $p<.05$; both z=-1.74, $p<.05$). In these conditions, the PDR group was more stable with the right hand than with the left, whereas the PDL group was more stable with the left hand than with the right (both covered PDR left 41.6 ms, right 36.5; PDL left 33.4, right 36.4; left covered PDR left 40.1 ms, right 36.2 ms. PDL median values very similar; left 39.2 ms, right 38.9 ms; other percentile scores, 25th 31.9 ms, 33.9 ms; 75th 47.7 ms, 49.2 ms, reveal the difference). When both hands were covered, the PDL group showed a significantly stronger correlation between RL and LR than the PDR group (PDL -.30; PDR -.25; z=-2.04 , $p<.05$).

It was mentioned above that in the PDR group, the right hand was significantly more stable than the left hand in the left-gallop / left-hand covered condition (Fig. 4.5A), whereas in the PDL group, the left hand was significantly more stable than the right in the same condition (Fig. 4.6A). Results for the correlation between interval-pairs were in line with these findings. Not surprisingly, in the left-gallop / left-hand covered condition the difference in

inter-tap interval variability between the hands differed significantly between the two groups (z=-2.50, p<.01), and the difference between the two correlation types was also significantly different for the two groups (Fig. 4.5 and 4.6, z=-1.74, p<.05). This is indicated by the black stars in Figures 4.5A and 4.6A. The correlation between RL and LR was (significantly) stronger than the correlation between LR and RL in the PDR group, whereas the latter was (non-significantly) stronger than the former in the PDL group. The correlation LR-RL was significantly stronger in the PDL group than in the PDR group in this condition (z=-2.12, p<.05). These results confirm the finding of opposite asymmetrical couplings in the asymmetrically affected PD groups in this condition, suggested in paragraphs 2.2.3 and 3.1.4. In both groups the primarily affected hand is leading and the relatively unaffected hand attempts to compensates for the variability in the affected hand.

The difference in variability between the left and right hand was significantly different between the groups, and the correlation between RL and LR was significantly higher in the PDR group, in the right-gallop / both hands covered condition (Fig. 4.5B and 4.6B; z= -1.89, p< .05). As mentioned earlier, the PDR group showed a more stable right hand, whereas the PDL group showed a more stable left hand. In line with the inter-tap interval variability results, the PDR group showed a significantly stronger correlation between RL and LR in the right-gallop / both hands covered condition (z=-2.12, p<.05). These findings suggest similar opposite couplings in this condition as in the left gallop / left hand covered condition. However, no effects within each group (between hands or interval-pairs) were found to support this idea.

4.4 Discussion

This study investigated bimanual coordination in individuals with and without Parkinson's disease and, more specifically, whether the coordination problems reported in PD are primarily the result of qualitative changes in inter-limb coupling or the enhanced asymmetry between the two sides of the body. In concordance with previous research (Byblow et al., 2000, 2002; Geuze, 2001; Johnson et al., 1998; Serrien et al., 2000a; Swinnen et al., 1997, 2000; Van den Berg et al., 2000) we found coordination problems in PD subjects compared to matched control subjects. These problems were apparent in general task performance (i.e., could subjects perform the task?) as well as in more detailed

analysis . Coordination, measured as the relative phase between the limbs, was more variable in PD subjects than controls. The underlying inter-tap intervals were also more variable in PD subjects. In the primarily left-affected PD subjects, coordination was also less accurate than in controls.

The control subjects in this study, ranging from 35 to 87 years of age, largely replicated findings in young adults in a previous study using the same set of tasks (Verheul & Geuze, 2003). Coordination in the control subjects was more stable and more accurate in the anti-phase pattern than in the left- and right-gallop, and inter-tap interval variability was also lowest in the anti-phase pattern. In the gallop patterns, a large phase shift was observed that was in both cases a shift away from the in-phase pattern in the direction of the anti-phase pattern. Previous studies have reported the phase shift in the in-phase and anti-phase pattern to be related to hand-preference (e.g., Treffner & Turvey, 1996), but in the gallop the phase shift appears to be related to hand-role (Verheul & Geuze, 2003).

Attention was directed to one or both hands by manipulating visual feedback of the hands and instructing subjects to attend to the visible hand(s). Similar to the young adults in the aforementioned study, the control subjects in this study showed little effect of the manipulation of attention. However, some significant effects involving attention were found, that were not found previously in the young adults. Firstly, coordination was less accurate when the left hand was covered than when both hands were covered, but no effects were found for coordination stability and phase shift. This is in contrast to findings in the in- and anti-phase pattern of Amazeen et al. (1997) and Swinnen et al. (1996), who reported effects of manipulating attention for both coordination stability and phase shift. An important factor in explaining the different results may be that Amazeen et al. and Swinnen et al. used more continuous movements tasks (pendulum swinging and circle drawing, respectively) that probably required more visual guidance.

Secondly, in the left-gallop the right hand was significantly more stable than the left hand when the left hand was covered and attention consequently directed to the right. In that same condition, the correlation between subsequent inter-tap intervals RL and LR was significantly larger than the correlation between intervals LR and RL (see Fig 4.4). The latter correlation was weakest in this attention condition. Similar results with respect to inter-tap interval variability and the correlation between intervals were found in the right-gallop, when both hands were visible. In the young adults investigated by Verheul and Geuze

(2003), both left-handers and right-handers showed a more stable left hand in the left-gallop and a more stable right hand in the right-gallop. It was suggested that this was caused by the ability to flexibly assign hand-roles to the hands depending on the task at hand. The left hand was assigned the hierarchically superior, or leading, hand-role in the left-gallop and the right hand was assigned that same role in the right-gallop. In the control group of the present study, no such general interaction between phase pattern and relative hand stability was found. On the contrary, in the left-gallop the right hand even became the significantly more stable hand or, as evidenced by the correlational results also, the hierarchically superior hand when attention is intentionally directed to that hand. It is important to note here that the control group consisted only of right-handers. It is plausible to assume that right-handedness was stronger in this group than in the right-handed young adults of the Verheul and Geuze (2003) study. Right-hand dominance on a standardized pegboard task has been found to increase with age (Weller & Latimer-Sayer, 1985). Handedness probably increases with age due to the proportionally larger amount of practice received by the preferred hand throughout life in comparison to the non-preferred hand (Kocel, 1980). A cohort effect due to the diminishing cultural pressure with respect to handedness may have added to this effect (Fleminger et al., 1977). It is therefore possible that the non-preferred hand is less likely to take on a leading hand-role in older subjects. When we compared the youngest ten with the oldest ten control subjects to test this prediction, we indeed found a right-hand lead more often in the older than in the younger adults, in particular when the left hand was covered and when both hands were visible. This may be related to the age-related reduced capacity to suppress intrinsic tendencies in bimanual coordination, that has been reported in the literature and are ascribed to cognitive functioning relying more on automaticity and less on feedback (Serrien et al., 2000b; Swinnen et al., 1998; Wishart et al., 2000). Future research could explore this issue further.

In order to discern between the two hypothesized mechanisms for loss of coordination in individuals with Parkinson's disease, we formulated a number of contrasting predictions for the two models. We will discuss each of these now.

Firstly, the enhanced asymmetry model predicted that the asymmetrically affected PD groups would perform worse than the symmetrically affected PD group. The impaired coupling model predicted the opposite. With regard to general task performance, the symmetrically affected group of PD subjects (PDS) performed better than the asymmetrically affected groups in the anti-phase, but

much worse in the two gallop patterns. Detailed analysis showed no significant difference between the symmetrically and asymmetrically PD subgroups in the anti-phase pattern for coordination stability or accuracy. The poor performance in the gallop cannot be understood from the enhanced asymmetry model, since asymmetry is presumably not enhanced in this group. PDS subjects may show motor problems in each hand, but coordination should not be particularly affected according to this model. Since the task for each hand (i.e., tapping with 800 ms intervals) remains the same over all patterns, but performance deteriorated markedly in the gallop patterns in the PDS group, a coupling based explanation must be sought for the poor performance of the PDS group in the gallop patterns. An explanation may be provided by the hierarchical coupling model. However, we must be considerate of the fact that this group is significantly older than the PDL group, and that this may have confounded results. In fact, as we argued before, age does seem to influence coordination characteristics considerably. Thus, we cannot conclude solely on the basis of these outcomes that the hierarchical coupling hypothesis is the more likely explanation.

Secondly, according to the enhanced asymmetry model, the primarily right-affected group (PDR) would perform superior to the primarily left-affected group (PDL) according, whereas the impaired coupling model predicted the opposite. The enhanced asymmetry hypothesis predicted the PDL group to perform worse than the PDR group, since in the former group the pre-morbid asymmetry (hand-preference) is further enhanced. The PDL group failed less often in the anti-phase pattern than the PDR group, but more often in both gallop patterns. Again, the interaction between group (affected side) and phase pattern cannot be explained by the enhanced asymmetry model and requires an explanation that involves coordination aspects. The detailed analysis of coordination characteristics (stability, accuracy and phase shift) in the PDL and PDR groups does not show that one group performed superior to the other in all conditions. The differences between the two groups are far subtler, but generally in favor of the PDR group. When the left hand was covered in the anti-phase pattern, the coordination in the PDR group was found to be more stable than coordination in the PDL group. When the right hand was covered, coordination in the PDR group was more accurate than in the PDL group. This is in contrast to the hierarchical coupling hypothesis that stated that the PDL group would perform better since the relatively unaffected hand (right hand) would be most successful at interlacing taps to create the required coordination pattern. Thus, this finding appears to

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support the enhanced asymmetry hypothesis. However, the discussion of the results for relative interval variability and for correlation between adjacent intervals below will provide an alternative explanation for the somewhat superior performance of the PDR group.

Thirdly, the enhanced asymmetry model predicted that the most affected hand would be less stable than the least affected hand, as a direct result of the asymmetric distribution of symptoms. In contrast, the hierarchical coupling hypothesis suggested that the affected hand would be more stable, due to the fact that the movements of the relatively unaffected hand would be subordinate to the movements of the affected hand (see Fig. 4.1). Variability in such a case would necessarily be larger in the interlacing hand than the timing (or pacing) hand. In the PDR group both hands were less stable than in controls, but the right hand (the most affected hand!) was significantly more stable than the left. Since this was not found in controls, this is strongly in favor of a hierarchical coupling for the PDR group. For the PDL group, the left hand was less stable than in controls, but the right hand was not and no significant differences were found between the left and the right hand over all conditions. However, we found a significant difference between the hands in one particular condition: in the left-gallop when the left hand was covered. In this condition, the left hand was more stable than the right hand. The correlation results partly confirmed these findings. A general effect for the PDR group was not significant, but in the left-gallop / left-hand covered condition the difference between the two correlation types was significantly different for the two asymmetrically affected PD groups. The correlation RL-LR correlation (see Fig. 4.2) was stronger than the LR-RL correlation in the PDR group, whereas in the PDL group the reverse was found. In sum, results suggest that in the PDR group, a hierarchical coupling may be prevalent. Within the PDL group, however, the strategy was found only in the left-gallop with the left hand covered, and appears not to be generally used.

Why was it used in this particular condition? First of all, the perceptual grouping of stimuli that are close to each other (Banks & Prinzmetal, 1976; Bregman & Reidnicki, 1975) would cause the first of two temporally close stimuli to be perceived as "leading" the other. Since perceptual relations are a main determinant of performance in the motor domain (Summers et al., 1989), it would be more natural to assign the leading or superior role to the first of two temporally close taps and the subordinate role to the second. This is the hand-role distribution that was indeed found in the young adults (Verheul & Geuze, 2003).

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This hand-role distribution was further encouraged by covering the left hand. It is probable that interlacing taps with a hand that is non-preferred, most strongly affected by Parkinson's disease and covered in addition to that, would have been most problematic. The complimentary question remains. Why was the hierarchical coupling strategy not used in any of the other conditions? An important clue was found in the effect of the hierarchical coupling strategy on coordination stability. In the PDL group, in the left-gallop with the left hand covered, the condition in which the PDL used the hierarchic coupling strategy, coordination was less stable than in other attention conditions in the left-gallop (note that this is opposite to the tendency in control subjects). Apparently, the hierarchical coupling strategy is not as beneficial for left-affected patients as it appears to be for right-affected patients. This difference in efficacy between the PDL and PDR group may be explained by a structural constraint, that favors the situation in which the left hand is subordinate to the right hand. All subjects in this study were (pre-morbidly) right-handed. There is evidence that pace-setting in bimanual coordination is a function that is at least partly lateralized in the left-hemisphere in right-handers (Viviani et al., 1998; Walter & Swinnen, 1990; Wyke, 1971), whereas the right-hemisphere is superior in the detection of simple visual stimuli (Marzi et al., 1991). Timing with the right hand and interlacing with the left hand is consequently a more natural and successful distribution of hand-roles than the reverse in right-handers. In healthy young adults, this constraint is apparent in multi-frequency tapping tasks, in which one hand is tapping faster than the other. In this situation, a strongly hierachical coupling strategy is adopted by subjects. It has been found repeatedly that reversal of hand-roles in such a task has a detrimental effect on performance (e.g., Byblow & Goodman, 1994; Peters, 1981, 1994). The hand-roles in the gallop may be reversed without a considerable loss of stability in young adults (Verheul & Geuze, 2003), but the results from the control subjects already suggests that this flexibility may be lost with age, and possibly also with disease.

This may also explain why the primarily right-affected subjects seem to be performing slightly better overall than the primarily left-affected subjects. The right-affected subjects may adopt a hierarchical coupling that is the optimal strategy for their situation, whereas the left-affected subjects do not have a similar, equally efficient strategy available. They can adopt the same (but mirrored) strategy, but in their case this is not an optimal solution.

Furthermore, the enhanced asymmetry model and the hierarchical coupling model predicted opposite phase shifts, but no main effect of group (affected side) was found for the phase shift. The PDR group showed a significantly smaller phase shift than the PDL group in the right-gallop / both hands covered condition, i.e., the right hand (most affected hand) was not as much advanced as in the PDL group. This is in favor of the enhanced asymmetry hypothesis, but it is unclear why this difference in phase shift only occurred in this particular condition. No tendencies could be discerned in other conditions.

The penultimate prediction concerned the left- and right-gallop specifically. The hierarchical coupling hypothesis predicted the left-gallop to be more stable than the right-gallop in the PDL group, and the right-gallop to be more stable than the left-gallop in the PDR group. The enhanced asymmetry model predicted the reverse. Results were not significant, but the existing tendencies in the data (see also Tables 4.4 and 4.5) support the hierarchical coupling model. However, if the groups use different strategies, i.e., one group shows an asymmetrical coupling as described by the hierarchical control model, but the other group does not, this complicates a simple comparison between the two groups on coordination level in order to deduct the underlying mechanism. Data on inter-tap interval variability and correlation are much more valuable in this respect, and coordination data is more relevant to assess the relationship between coupling strategies and coordination.

Finally, the enhanced asymmetry model predicted that directing attention to the relatively unaffected hand would be beneficial for coordination stability, analogous to the effect of directing attention to the preferred hand in adults without PD that is reported in the literature (Amazeen et al., 1997; Swinnen et al., 1996). The hierarchical coupling model made no specific predictions about the effect of manipulating attention. Our results showed that the strongest difference in coordination stability between the PDL group and the control subjects was found for the condition in which the right hand was covered, but between the PDR group and the controls when the left hand was covered. Also, anti-phase coordination was more stable in the PDR group than in the PDL group when the left hand was covered. Thus, when attention was directed towards the left, this benefited coordination in the primarily left-affected PD group, and when attention was directed towards the right, this benefited the primarily right-affected PD group. This is opposite to the prediction from the enhanced asymmetry model, and as such gives support for an alternative model.

In sum, the subjects with Parkinson's disease performed worse than the matched control subjects in terms of coordination stability, accuracy and the stability of the inter-tap intervals. Findings in the control subjects did not fully replicate previous results for young adults (Verheul & Geuze, 2003), suggesting that the ability to flexibly change hand-roles in response to task-asymmetry may become less with age. Hardly any support for the enhanced asymmetry hypothesis has been found in the present study. Clearly, the nature of inter-limb coupling has to be addressed in any theory of coordination in Parkinson's disease. The symmetrically affected patients performed particularly poorly in the gallop patterns, but age cannot be excluded as a confounding factor. For the primarily right-affected PD patients the hierarchical control model was largely supported, although individual deviations from this control strategy may have occurred in specific conditions. In the primarily left-affected PD group, the proposed hierarchical control model was only apparent when the left hand was covered in the left-gallop, and was associated with a marked decrease in coordination stability. This unpredicted result was hypothesized to be due to the lateralization of timing and visual monitoring functions in the (pre-morbidly) right-handed subjects. The arisen issues of age and pre-morbid hand-preference in relation to bimanual coordination deserve further exploration in future research.

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**Summary and
General Discussion**
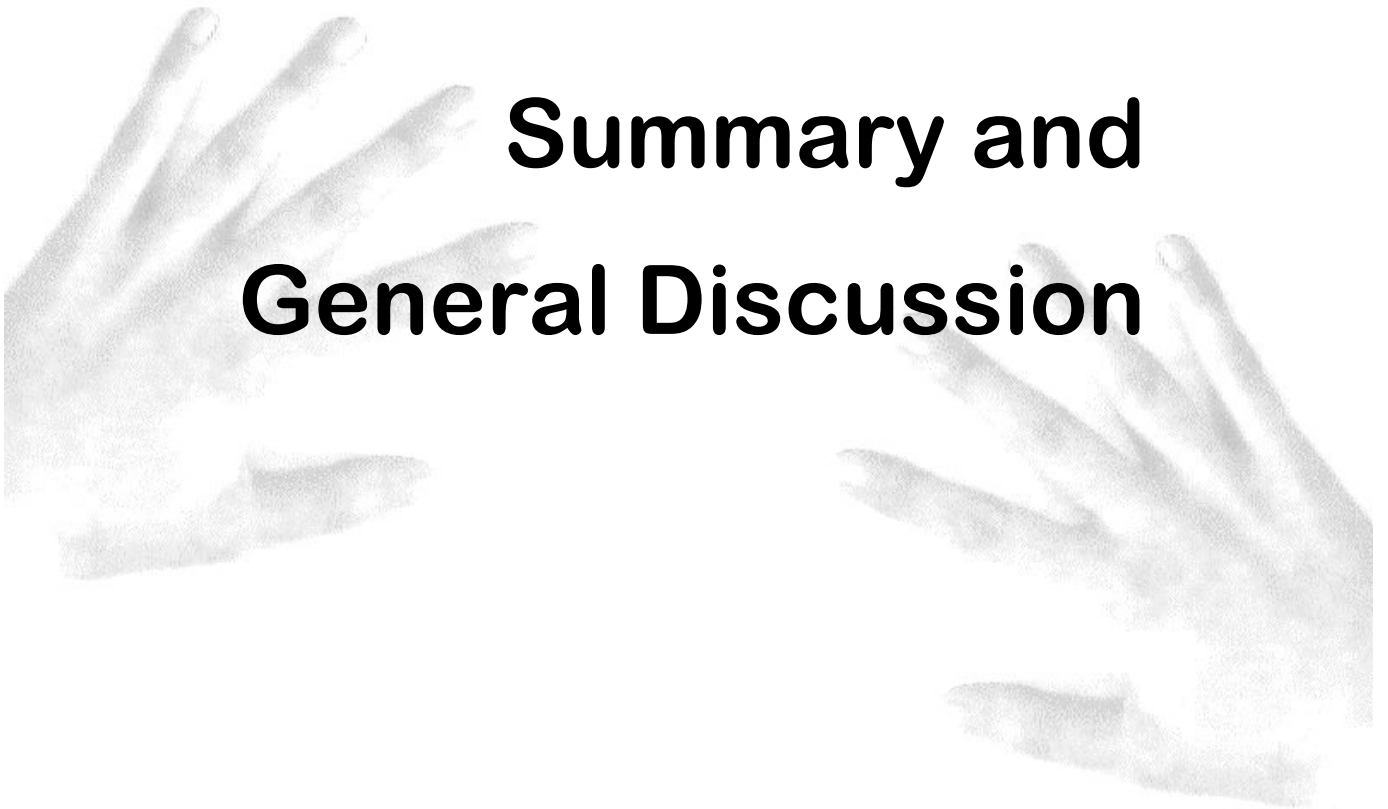
5.1 Constraints on Coordination

This thesis investigates the role that intrinsic and task constraints play in the rhythmic coordination of two hands. Within the dynamic systems approach to motor coordination, constraints are seen not just as factors influencing motor control, but as essential prerequisites for the emergence of motor coordination. Constraints set the conditions within which self-organization can take place. They can be defined as the boundaries which limit the number of co-ordination states available to a dynamical system at any instance of its search for an optimal state of organisation (Newell, 1986).

This approach stands in sharp contrast to any notion of "prescription", in the sense that there is not a location in the brain where an entire motor pattern is represented. Instead, control is *distributed*. In walking, for instance, the length and mass of the limbs, the external forces acting on the system, and the neuro-muscular system together generate the pattern that we recognize as "walking". Thus, a walking pattern is not simply represented in the brain, but emerges from the interaction between brain, body and environment. The emphasis the dynamic systems approach to motor control places on multi-causality has an important implication for research into motor control: the various elements together causing motor coordination should not be investigated in isolation, but in interaction. In this thesis three experiments have been reported that were designed to look at the interaction between organismic (or individual) and task constraints, rather than the effects of those constraints in isolation.

In *Chapter 2*, a study was reported that investigated the interaction between musical experience and so-called "behavioral information" in various coordination patterns. Intention, memory and external pacing signals provide such behavioral information. It can be regarded as a constraint on motor coordination that complement the "intrinsic dynamics", i.e., spontaneous coordination tendencies such as the preference to move two limbs in synchrony, especially at higher frequencies.

Intrinsic dynamics have been studied much more extensively than behavioral information. The intentional, goal-directed nature of human motor behavior has been disregarded somewhat in the past, but has recently regained interest (Riley & Shockley, 2003). A possible explanation for the apparent reluctance to step into this area of research may be the paradoxical nature of dynamic studies into

cognition. The dynamic systems approach has explicitly dissociated itself from the information-processing approach to motor control, and yet, investigates the effects of concepts such as attention with traditional information-processing paradigms such as the dual-task paradigm (e.g., Temprado et al., 1999; Zanone et al., 2001). However, the dynamic systems framework legitimizes interest in cognitive effects on coordination to the same extent as it legitimizes interest in biomechanical or physiological effects. Through the concept of behavioral information, the arbitrary representation of information is avoided (Schöner, 1989). Analysis of stability properties of coordination patterns reveals relevant information by its effect on coordination itself. The common language of dynamics ensures continuity with biomechanical and physiological concepts (Schöner 1989; Schöner & Kelso, 1988b).

The study described in Chapter 2 compared a group of musically trained individuals (*N*=10) and a group of individuals that had received no musical training throughout their life (*N*=10). Both groups performed a finger-tapping task with different patterns of coordination: in-phase, anti-phase and left and right gallop. At the beginning of each trial, movements were paced by a metronome. Subjects were instructed to continue tapping after the pacing had stopped. Halfway through the trial, a visual signal indicated that the subjects had to switch promptly to another, pre-specified, pattern. The task was first performed under a neutral set of instructions (e.g., "tap in an alternating manner"), and then under a set of instructions that emphasized the 'ecological nature' of the coordination patterns (e.g., "imagine your fingers being the front legs of a trotting horse"). Musically trained subjects showed more stable and more accurate coordination than subjects without musical training. The effect of memorized behavioral information (the gait analogy) was not different for the two groups. However, it did affect stability of coordination in the different phase patterns differently, with a positive effect on the anti-phase and the 90°-phase pattern, but a negative effect on the in-phase pattern. Switching times were mostly in line with results for relative phase variability.

In addition to these results, we noted signs of asymmetry. Firstly, subjects showed a strong intra-individual preference for one type of gallop. Moreover, their choice of gallop was strongly related to the switching strategy used. The switching strategy subjects chose was not only consistent over switches from and to the gallop, but extended to switches between in- and anti-phase. Due to the design of the present study (only two left-handed subjects), no conclusion could

be drawn as to whether cerebral dominance (i.e., hand-preference) could be a factor in this. Some suggestions have been reported in the literature to extend the symmetric coordination model so that it can account for coordination asymmetries. However, none of these could fully explain the asymmetry found in the present study. The results call for a systematic study of the interaction between intrinsic and task asymmetry (e.g., the gallop).

Chapter 3 aimed to investigate the interaction between intrinsic and task asymmetries in the bimanual gallop pattern. A group of left-handers (N= 11) was compared with a group of right-handers (N=13) with regard to their performance of the bimanual gallop pattern. For comparison, the anti-phase pattern was included. The task was again a continuation task, but now the subjects were instructed to tap the same pattern as constantly as possible for the duration of the trial. Previous research has shown that in multifrequency tapping the hands tend to have different hand-roles: the faster hand functions as 'timer' while the slower hand interlaces its taps so that the required coordination pattern arises (Summers et al., 1993). In multifrequency tapping, the distribution of the hand-roles over the hands (i.e., the hand arrangement) has a large effect on performance. Coordination suffers greatly when the non-preferred hand is given the leading hand-role (the timer). However, it cannot be concluded from these studies that the difference in hand-roles (leading, interlacing) causes the deterioration of performance, since tapping frequency varies with hand-role. In the gallop pattern these two elements can be unraveled, as both hands tap at the same frequency, and asymmetry only exists on the level of the coupling between the hands. We instructed subjects to tap the anti-phase pattern and both types of the gallop under symmetrical and asymmetrical visual feedback conditions, since literature has suggested that asymmetrical feedback may strengthen the effects of intrinsic asymmetry (Amazeen et al., 1997; Swinnen et al., 1996).

Using various techniques to investigate the same hypothesis, it was shown that the gallop pattern is hierarchically controlled, i.e., the hands are asymmetrically coupled. The hand that was a quarter of a cycle ahead was found to exert a stronger influence on the lagging hand than vice versa. Also, the intertap intervals of the advanced hand were less variable. The finding that performance of the non-preferred hand was more stable than performance of the preferred hand when the non-preferred hand was forced to adopt a leading hand-role, implies that handedness in bimanual coordination is task-dependent. Coordination was found

to be equally stable in both hand arrangements, i.e., no effect of hand-preference was found. This finding suggests that the deterioration in performance associated with hand arrangement in multifrequency tasks may be due to the difference in velocity between the hands rather than the difference in hand-roles.

In *Chapter 4* the same experimental paradigm was used to study the interaction between intrinsic asymmetry and task asymmetry in Parkinson patients. It has been reported that Parkinson patients show bimanual coordination problems (Byblow et al., 2000; Geuze, 2001; Johnson et al., 1998; van den Berg et al., 2000). However, it is not clear to what extent these problems are a direct result of central coupling problems and to what extent they are an indirect result of asymmetry of symptoms. In the studies that identified coordination difficulties, patients with mild Parkinsonism were investigated. In these patients, the symptoms (e.g., rigidity, tremor) are often much stronger on one side of the body than on the other. Bimanual coordination dynamics is likely to have changed as a result of this pathologically enhanced asymmetry. In our study, a group of premorbidly right-handed Parkinson patients was subdivided into three groups: symmetrically affected patients (*N*=10), primarily left-side affected patients (*N*=10) and primarily right-side affected patients (*N*=10). A healthy control group (*N*=30) was also included in the study. The control group (mostly elderly subjects) appeared less flexible than the young right-handed adults from the previous study in adopting different hand-roles dependent on the task. This is linked to an increase in intrinsic asymmetry, i.e., hand-preference, with age. Data of the subjects with Parkinson's disease provided very little support for the model based on enhanced biomechanical asymmetry, but do support the idea of a changed inter-limb coupling, although not fully in line with the proposed model. Pre-morbid hand-preference appears to be an important structural constraint on the coupling strategies available to the subjects.

5.2 The relationship between asymmetry, variability and flexibility

The difference between the results described in *Chapters 3 and 4* shows how the effect of task asymmetry is influenced by intrinsic coordination dynamics. In Chapter 3, it has been argued that hand-role can have a stronger effect on manual asymmetry than hand-preference. Depending on the task, the organization of coordination is different and the manual asymmetry changes. The importance of

the task-context stands out as a determining factor. In contrast, however, in Chapter 4, pre-morbid hand-preference restricts the coordination strategies available to Parkinson patients, and therefore influences their coordination negatively. Also, the mostly elderly control subjects appear not to show the flexible re-organization of coordination in response to the changes in task-context that the right-handed young adults in Chapter 3 showed. Apparently, in the older adults with and without Parkinson's disease intrinsic asymmetry had a stronger effect than task asymmetry, whereas the opposite was found for young adults.

In the literature a symmetric coordination system is associated with "absolute coordination" or phase locking, whereby the component oscillators of the system are rigidly coupled. Flexibility arises through breaking the symmetry of the coordination dynamics (e.g., Carson, 1993; Kelso, 1994; Kelso & Ding, 1993) by intrinsic or task-related factors such as hemispheric asymmetry or differential loading of identical limbs. Competing tendencies give rise to a complex of phenomena (intermittency, phase slippage, etc.) collectively called "relative coordination" and expressed in phase attraction, but not phase locking. Kelso and Ding (1993) explain relative coordination with a simple example: When a father walks along with his small child, the father must slow down or the child must skip steps, because of their intrinsically different cycle periods. Although the father and child will have a tendency to couple their movements, these will only be relatively synchronized. Experimentally, a lower degree of intra-limb joint coupling in a circle-drawing task (in the non-preferred limb compared to the preferred) has been linked to a more efficient response to environmental contingencies (Carson, 1993; Van Emmerik & Newell, 1990).

However, as present data shows, "loose" coordination may not only provide flexibility, but also coincide with uncontrollability. The relative coordination dynamics described by Kelso & Ding (1993) and others may not only be a source for flexibility, it may also be the cause of diminished control. Intermittency and phase wandering are not always desirable. Often we require stability; a task may demand us to stay in one coordination pattern, and not to switch between patterns. What if the system is too unstable for efficient relative coordination? The logical

control strategy would be to "freeze" degrees of freedom and revert to the basic coordination patterns, in-phase and anti-phase, the latter only at low velocities.[1]

The idea of limited coordination possibilities in Parkinson patients finds support in the literature. In addition to the repeated finding of increased relative phase variability for interlimb coordination (e.g., Geuze, 2001; Johnson et al., 1998; van den Berg et al., 2000; and the present study), there are reports of inflexible behavior, i.e., the inability to uncouple movements and the related inability to switch between coordination patterns. Van den Berg et al. (2000) reported that Parkinson patients, when asked to perform movements with one arm, showed mirror movements with the contralateral arm. Mirror movements are typically observed in children (for a review, see Geuze, 2004), for instance in the movement of the tip of the tongue when a novice writer concentrates on his or her writing. Mirror movements indicate involuntary, or in other words too much, coupling. Note that we observed two Parkinson patients having difficulty with tapping anti-phase, tapping a 1:2 pattern instead, which can be considered as incorporating mirror movement. Another sign of inflexibility in Parkinson patients is reported with regard to trunk rotation while walking (van Emmerik et al., 1999). Normal trunk coordination is characterized by an in-phase coupling of shoulder rotation and hip rotation in the horizontal plane at low velocities, and anti-phase at high velocities. Beyond a certain velocity, it is necessary that the shoulder counteracts the rotation of the hip that accompanies the forward-swing of the leg, in order to maintain balance. Parkinson patients, however, tended to remain in an in-phase coordination pattern, in spite of the increase in velocity of the treadmill on which they were walking. Thus, inter-limb coordination in adults with Parkinson's disease is paradoxically both more variable and more rigid (i.e., inflexible) than coordination in adults without Parkinson's disease.

In sum, Kelso and colleagues have pointed out that absolute coordination may be too stable, and not effective for task-sensitive motor control. However, the positive (by times lyrical) description of the effects of asymmetry (e.g, Kelso, 1994a) seems to apply primarily to the healthy, young adults, and far less to the older adults with and without Parkinson's disease. The present data show that too much "flexibility" could mean a loss of coordination possibilities. The balance

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[1] The Parkinson's disease symptom bradykinesia (moving slowly) can be understood within this framework as compensatory behavior. This is not a novel idea, it has been suggested before by Martin et al. (1994).

between stability or controllability on the one hand, and flexibility or the ability to respond to task requirements with adaptive motor behavior on the other hand, is apparently a delicate one.

Understanding how asymmetry can lead to flexibility as well as inflexibility is half the story. It is also important to understand what the nature is of the asymmetry causing the inflexibility in older adults with and without Parkinson's disease. The results in Chapter 4 suggest that the coordination deficit in Parkinson patients is the result of an impaired coupling rather than an indirect result of biomechanical changes (e.g., rigidity) per se. This coupling deficit may be linked to attentional difficulties. As explained in Chapter 4, the reduced functioning of the supplementary motor area in Parkinson's disease is likely to lead to a type of motor control that requires more sensory feedback and a higher allocation of attention. In some tasks, the attentional cost may be too high, causing deterioration of performance. Alternatively, the ability to allocate attention effectively may itself be affected. The basal ganglia, the structure that is affected in PD patients, have been hypothesized to play a role in selective attention and its flexibility (Ravizza & Ivry, 2001). Indeed, Parkinson patients show perseveration in mental as well as motor tasks (Bowen et al., 1975; Inzelberg et al., 2001). The attention test used in these studies is the Wisconsin Card Sorting test (e.g., Nelson, 1976). In bimanual coordination, a similar inability to shift attention was found in PD patients (Horstink et al., 1990). These patients were asked to draw triangles with the dominant hand and squeeze a rubber bulb with the nondominant hand. After correcting for baseline single-handed performance, the amplitude of squeezing was found to be significantly reduced in PD patients. A number of studies have shown that motor learning, although still possible, is impaired in PD, especially when visual feedback is withheld (Swinnen et al., 00; Verschueren et al., 1997). The effects of visual feedback in these studies, as well as in the study described in Chapter 4, could point to a relationship with attention. In young adults (Chapter 3), hardly any effect of attention was found, whereas the most effects in Chapter 4 were found within specific attention conditions.

Aging in healthy individuals is also typically characterized by a decrease in attentional capabilities and a lower ability to acquire new skills, although to a lesser extent than in PD subjects (the studies reported above used age-matched controls, that outperformed the patients). Wishart et al. (2002) showed that older adults needed more augmented feedback to learn a continuous bimanual gallop pattern than young adults. They hypothesized that older adults have a decreased

ability to focus attention to the salient aspects of the task. Lateralization in healthy adults has also been theoretically linked to attention (Peters, 1994). Since laterality increases with age (Weller & Latimer-Sayer, 1985), the attentional bias would increase as well. This could explain why hand-role was determined more by intrinsic than task-related factors in the older adults of Chapter 4. Finally, motor lateralization has been linked to the nigrostriatal dopamine system (de la Fuente-Fernàndez et al., 2000), which provides another link between changes in coordination with aging and changes in coordination caused by PD.

In conclusion, the mechanism underlying the impaired coupling in PD subjects may also cause the change in coordination with aging and the coupling characteristics of PD patients may be of a quantitative rather than a qualitative nature, with PD patients further along the continuum between flexible stability and inflexibility. This idea finds further support in our finding that coordination stability did not differ between the PD subgroup that was significantly older than the other PD subgroups, and their age-matched control subjects. By contrast, coordination in the other two PD subgroups was significantly less stable than in their age-matched control groups. This could not be explained by superior performance in the older PD subgroup, since this group showed in fact less stable coordination than the other two groups. Thus, the difference in coordination stability between PD patients and healthy individuals appears to diminish with age.

5.3 The dynamic systems approach to motor coordination

The dynamic systems inspired research into rhythmic interlimb coordination forms a strong research program, as judged by qualifications defined within the field of philosophy of science. Kuipers (1997) makes a distinction between four types of research programs, based on their internal goal: descriptive, explanatory, constructive (or design) and explicative. The dynamic approach to rhythmic inter-limb coordination is an explanatory research program, since it explains individual facts (e.g., phase transitions), generates predictions (e.g., patterns of variability) and has introduced a new set of theoretical terms (synergetics). In terms of strength, the program falls within the highest category according to Kuipers' criteria. Research within the program not only shares a domain (inter-limb coordination) and an idea (self-organization), but also a model that functions as a positive heuristic (the Haken-Kelso-Bunz, or HKB model). This type of program

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is maximally capable of internally steering its research. Of course, one can question the strength of the idea and the model itself, but the sustained (and growing) interest in the program over the last two decades suggests that it is more than a "freak of fashion". This growing interest is evidenced among others by the increased referencing in SCI and SSCI rated journals to the journal article in which the HKB model was first presented (Fig 5.1).
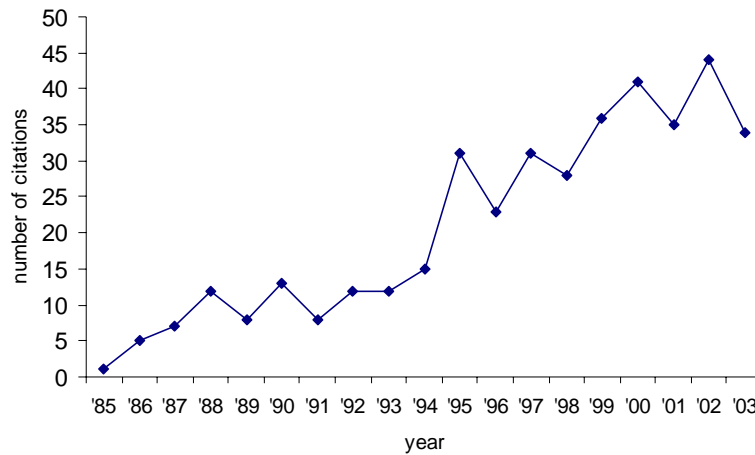

Figure 5.1. Citations per year of the Haken et al. (1985) article, in which the HKB model was first presented. Only citations in SCI/SSCI-rated journals were counted. SCI = Science Citation Index (SCI) and the Social Sciences Citation Index (SSCI).

The dynamic approach to motor coordination has passed through the typical phases of an explanatory research program. The idea of the program arose against the background of seemingly unsolvable problems within another program (the information-processing approach to motor coordination – see introduction). Next, the idea was elaborated for various contexts and subdomains in the so-called evaluation phase (see introduction). As a result of these studies, the HKB model has been extended and refined. However, this elaboration phase does not represent the final stage of a research program. A critical last stage of an explanatory research program is the external or application stage. This stage is entered when the core theory of the program is generally accepted and clarity exists about the extent to which it can be assumed to be true. The theory can then

be applied to questions in a different research area (Kuipers, 1997). At present, self-organization and the tools of synergetics are not generally accepted as theory and method in the study of human motor control. The situation might be about to change, though, for instance in the field of motor development, where the seminal work of Thelen & Smith (1994) has now made its (modest) entry into popular introductory textbooks of life-span motor development (e.g., Haywoods & Getchell, 2001). Similarly, synergetics is discussed in textbooks on human motor control, albeit under the heading of "new" or "alternative" approach (Rosenbaum 1991; Abernethy et al. 1996). At the same time, however, an opposing trend can be observed in the tendency towards materialistic reductionism. This is the (ontological or methodological) conviction that the explanation of phenomena can be found in physical structure. Thus, the explanation of motor behavior is sought in genetic material or in cells, or molecules, within the brain. For example, a recent inaugural speech of a newly appointed professor at the University of Amsterdam was titled "Get rid of psychology", and consisted of a plea for a molecular approach to the understanding of human behavior. From a dynamic systems perspective, studying neural processes in great detail is essential, but to understand these processes it is essential to understand the relationship between the brain and its environment. The brain did not merely evolve to register representations of the world; rather, it evolved for adaptive action and behavior (Kelso, 1995). In other words, the principles of brain functioning need to be understood. In sum, the dynamic approach to motor coordination makes up a strong research program, but has to compete with a reductionistic tendency in modern research.

5.4 A re-appreciation of learning and re-learning

The dynamic perspective has important implications for the way that development and learning in a normal and pathological movement system are approached. First of all, inter- and intra-individual variability are meaningful characteristics of a dynamic developmental or learning process. Children learn by exploring various coordination patterns and selecting the most functional one within the prevailing constraints (Thelen & Smith, 1994). For instance, the motor milestone of crawling is achieved in many different ways by different children. The coordination patterns displayed by the children are adapted to deal with a particular environment (e.g., the "sea lion crawl" for slippery floors). Moreover, it is

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achieved at a wide range of ages, roughly between the 5th and the 10th month of the infant's life. The speed at which skills are learned in infancy also varies greatly between children and between skills within a child (Gallahue & Ozmun, 1995). Thelen and Smith (1994) have argued that perceptual and cognitive development is guided by the same process of exploration and selection. Since structure and function are mutually constraining aspects, it would be incorrect to conclude that one is the cause and the other the effect. The dynamic interaction between structure and function guides the developmental process.

The notion of self-organization of motor coordination implies that variability should be valued (Davids et al., 1998). Teachers and coaches should allow, or rather, encourage, learners to explore various coordination patterns and minimize verbal instruction. Since the optimal motor pattern depends on individual constraints, among others, it is important to recognize the individuality of solutions. It has been shown that instructions focussing on the desired outcome of a movement (e.g., the trajectory of a kicked ball) are more effective in teaching than instructions focussing on the movements of body parts (e.g., Wulf et al, 1998, 2001). Learning an effective coordination pattern can be guided by cleverly designing the learning environment, so that the learner will "automatically" pick up the desired skill. For example, wearing a fingerless glove will encourage a novice basketball player to dribble with the tips of the fingers instead of the palm of the hand. This idea extents to informational aspects of the task. Taking away or distorting one source of information automatically forces the learner to search for other sources of information. For example, having a basketball player wear a pair of glasses of which the bottom half is painted black, will encourage the player not to look down. When dribbling, the player will be forced to search for other information sources than visual information to control the ball and is likely to discover the use of proprioceptive information. Vision can then be used to assess the game situation, e.g., the position of the surrounding players. Being able to use different sources of information to guide a particular action has obvious advantages in an unpredictable game situation.

The notion of "multiple realizability" (Bernstein, 1967) implies that a movement solution can be generated in more than one way. Various organizations of the underlying components may lead to approximately the same movement. The recognition of the individuality of solutions becomes particularly relevant within the context of rehabilitation or re-learning after the (neuro)motor system has been changed as a result of an accident or disease. It implies that the optimal

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movement pattern in an affected motor system not necessarily equates to the optimal pattern in a "normal" motor system. Changed motor patterns observed in patient groups may be considered adaptive to a primary disorder. They may represent the optimal motor pattern within the changed constraints (Latash & Nicholas, 1996). As Latash & Anson (1996) have phrased it:

"What are normal movements in atypical populations?" (p. 55)

For instance, co-contraction in a spastic population may not be the problem, but the best solution within the constraints of the altered system (Levin et al., 2000). Muscles within the spastic motor system are constrained by a stretch reflex threshold within the physiological range of motion. This means that when a muscle is stretched beyond a certain angle by active or passive movement, the muscle will start to contract. Voluntary movement in such a system necessarily implies co-contraction of antagonistic muscles in certain ranges of movement. It may be the case, then, that selective strength training of the least spastic muscles (the extensors of the arms and the flexors of the legs) generates a neuromuscular system that is better equipped to deal with the extant spasticity. Thus, instead of trying to minimize co-contraction since it is "not normal", it may be better to focus on building a system that is most successful at generating voluntary movements with the given constraint of co-contractions. Therapeutic interventions should not aim to restore movement patterns to "as normal as possible" but should aim to aid the system of movement production to develop optimal adaptive coordination patterns (Latash & Nicholas, 1996).

In the study described in Chapter 4 of this thesis, this point is illustrated by the asymmetric coupling strategy that the primarily right-affected Parkinson patients adopted. It was found that these patients tapped significantly more stable with the right (i.e., the most affected!) hand than with the left hand. Moreover, an analysis of the correlation between adjacent intertap intervals revealed that the movements of the left hand were more strongly dependent on the movements of the right hand than vice versa. These findings indicate that this patient group adopted a strategy in which the most affected hand tapped at regular intervals, and the relatively unaffected hand created the required coordination pattern by interlacing taps at a quarter (right-gallop), half (anti-phase) or three-quarters (left-gallop) of the cycle of the affected hand.

In terms of tapping variability, both hands of the primarily right-affected patient seemed to be performing poorly compared to control subjects. This is in contrast to the primarily left-affected patients, who performed worse than control subjects only with the left hand. However, as explained above, the "poor performance" of the left hand in primarily right-affected patients in bimanual coordination should be interpreted as an adaptive movement pattern.

A frequently used method in therapeutic interventions for coordination problems is breaking down the skill in small parts (isolated movements), before combining them again. However, if coordination is the problem, then the aim should be to optimize coordination within the constraints of the system. Since the system is altered, this may imply a functional re-organization of movement components. In line with the constraints-led approach in skill acquisition (Davids et al., 1998), patients should be encouraged to explore and optimize coordination strategies by a process of trial-and-error. It is the role of the therapist to guide patients to the most effective coordination pattern (for example by manipulating attention or the required coordination pattern). To be able to do this, we have to understand the nature of the coordination problem in patient groups.

## 5.5 Future research: Multi-degree of freedom movements

Most dynamically inspired coordination studies so far, including the studies described in this thesis, have investigated one- or few-degree of freedom systems, whereas many actions in real life involve many degrees of freedom. For instance, when one walks towards a table and picks up an object, legs, trunk and arms are involved in interaction with each other. Control parameters of the coordination pattern may include factors like the fragility and weight of the object (Savelsbergh et al. 1996; Steenbergen et al., 1995). Little is known about the coordination dynamics of such multi-degree of freedom movements. Although the assumption is that the coordination of these movements is also governed by non-linear dynamics and will display the same phenomena as displayed in simple tapping tasks, this needs to be proven.

The number of studies that look at coordination dynamics in real-life multi-degree of freedom tasks is slowly increasing. In a real-life task of catching with both hands, it was shown that the hands are timed in an in-phase manner (Tayler & Davids, 1997). Since the ball was sometimes projected not at the center of the chest, but at the right or left shoulder area, this implied the limbs sometimes

moved at different speeds to maintain an in-phase coordination pattern. When learning a movement involving multiple degrees of freedom, joint movements tend to be strongly coupled initially, i.e., joints are moved in an in-phase or anti-phase coordination pattern. Novice coordination patterns for skills such as slalom-like moving on a ski-simulator, serving in volleyball, kicking in soccer and throwing darts have been found to be characterized by high cross-correlations between the angular displacements and velocities of the joints involved (Anderson & Sidaway, 1994; McDonald et al., 1989; Temprado et al., 1997; Vereijken et al., 1992). With practice, those cross-correlations decrease and ranges of motion increase. In the soccer kick, for example, the coordination pattern changes from a simultaneous onset of flexion of the hip and extension of the knee to a phase-lagged onset. This way, the knee is able to take greater advantage of the velocity generated at the hip and maximizes the velocity of the foot (Anderson & Sidaway, 1994).

There are indications that more complex movements may show a somewhat different dynamics than one-degree of freedom movements. Whereas transitions from anti-phase to in-phase are a normal phenomenon in finger flexion/extension tasks when increasing frequency, they do not normally occur in pendulum swinging. Pendulum swinging requires abducting/adducting of the wrists. However, it has been noted that, at higher frequencies, there is an increased contribution of wrist flexors and extensors. (Kelso, 1998). The flexors and extensors cause the movement to become more spherical, and may somehow prevent the transition to in-phase. Thus, recruitment (and suppression) of biomechanical degrees of freedom at the component level may change the dynamics (Kelso et al., 1993). This is in line with the remarkably gradual transitions that Van Emmerik and Wagenaar (1996) observed in trunk rotations when subjects walked with increasing velocity. These findings suggest that results from one-degree of freedom studies cannot simply be generalized to multi-degree of freedom situations. More research is needed to gain insight into the motor coordination underlying "real" actions.
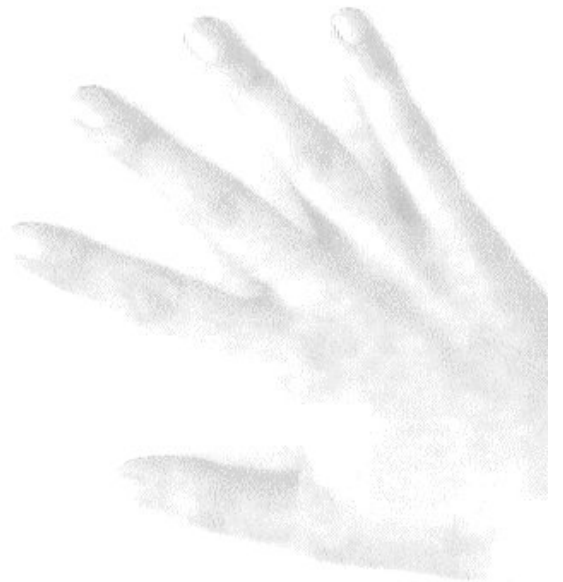
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Appendix I

Hand-preference questionnaire
(van Strien & Bouma, 2000; translated from Dutch; reprinted with permission)

This list contains questions regarding the different aspects of left- and right-handedness. Please answer as accurately and completely as possible.

Writing hand
Which hand do you use to write?   left / right / forced to use the right hand in school

Hand-preference
Below, a number of activities are mentioned that one can perform with either the left or right hand. Please indicate which hand you normally use for each of these activities. If you do not know the answer, imagine performing the task. Only if you have no preference, tick 'both'.

1. Which hand do you use to draw?	left / right / both
2. Which hand do you use to brush your teeth?	left / right / both
3. Which hand do you use to hold a bottle opener?	left / right / both
4. Which hand do you use to throw a ball far away?	left / right / both
5. Which hand do you use to hammer a nail?	left / right / both
6. Which hand do you use to hold a racket (for example when playing tennis)?	left / right / both
7. Which hand do you use to hold a knife when cutting a rope?	left / right / both
8. Which hand do you use to stir with a spoon?	left / right / both
9. Which hand do you use to hold an eraser when rubbing out something?	left / right / both
10. Which hand do you use to hold a match while striking it?	left / right / both

Scoring
left = -1, right = +1, both = 0.

Appendix II

Geriatric Depression Scale (GDS) – Short Form
(original 30-item form Brink et al., 1982/Yesavage et al., 1983; short form Sheikh
& Yesavage, 1986; Dutch translation Bleeker et al., 1985)

This questionnaire contains questions you can answer with "yes" or "no". Read the questions and think of the answer you would give. You give the answer that best fits how your have felt over the past week (including today). Please circle the answer you chose. It is important that you answer all 15 questions.

1. Are you basically satisfied with your life?	Yes / No
2. Have you dropped many of your activities and interests?	Yes / No
3. Do you feel that your life is empty?	Yes / No
4. Do you often get bored?	Yes / No
5. Are you in good spirits most of the time?	Yes / No
6. Are you afraid something bad is going to happen to you?	Yes / No
7. Do you feel happy most of the time?	Yes / No
8. Do you often feel helpless?	Yes / No
9. Do you prefer to stay at home, rather than going out and doing new things?	Yes / No
10. Do you feel you have more problems with memory than other people?	Yes / No
11. Do you think it is wonderful to be alive now?	Yes / No
12. Do you feel pretty worthless the way you are now?	Yes / No
13. Do you feel full of energy?	Yes / No
14. Do you feel that your situation is hopeless?	Yes / No
15. Do you think that most people are better off than you are?	Yes / No

Scoring
Questions 1, 5, 7, 11, 13: "yes" = 0, "no" = 1; all other questions "yes" = 1, "no" = 0.
Scoring intervals: 0-4 no depression, 5-10 mild depression, 11+ severe depression.

The GDS may be used freely according to the authors.

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Appendix III

Items of the motor examination part (part III) of the
Unified Parkinson's Disease Rating Scale (UPDRS)
(Fahn & Elton, 1987)

Speech
Facial Expression
Tremor at rest: face, lips, chin
Tremor at rest: hands*
Tremor at rest: feet*
Action tremor*
Rigidity neck
Rigidity upper extremity*
Rigidity lower extremity*
Finger taps*
Hand grips*
Hand pronate/supinate*
Leg agility*
Arise from chair
Posture
Gait
Postural Stability
Body Bradykinesia

* These items should be assessed for the left and the right side of the body
separately.

Scoring

The neurologists involved had access to a detailed description of the items and the
scoring per item. Global scoring: 0 = normal / absent, 1 = slight / minimal, 2 = mild /
moderate, 3 = moderate / severely impaired, 4 = marked / can barely perform the task.
Maximum score = 108.

Appendix IV

Multi-level regression analysis

This appendix has a twofold aim. First of all, the aim is to provide a brief explanation of the statistical method used in the study presented in Chapter 2. A complete explanation of the method was beyond the scope of that chapter. However, since the method is relatively unknown, a tutorial of the method is provided here. This tutorial is based on a number of introductory papers (Albandar & Goldstein, 1992; Beacon & Thompson, 1996; Hoeksma & Koomen, 1992) and two books about multi-level modelling (Kreft & de Leeuw, 1998; Snijders & Bosker, 1999). The reader is referred to these sources for more information on the method.

Furthermore, the method will be put in the context of recent changes in theory building in the field of motor development and skill acquisition. New insights into the nature of the developmental and learning process have re-directed the focus of attention to a new type of question. I will argue that it is exactly this type of question for which multi-level regression analysis is particularly useful. This discussion is based on an oral presentation at the 7th European Workshop on Ecological Psychology (Verheul, 2002).

The Method

Multi-level regression analysis is a specific type of regression analysis. In order to explain this type of analysis, it is compared with simple regression analysis. Simple regression analysis aims to predict the level of a variable Y from a variable X. Figure A.1 depicts an imaginary data set (the dots). A regression model is fit onto this data (the line). The best fitting model is determined using a method such as the '(ordinary) least squares method' (see for example Field, 2000, for an explanation of this method). The most basic regression model proposes a linear relationship between X and Y:

$$Y_i = \beta_0 + \beta_1 x_i + R_i \qquad\qquad (1)$$

in which β_0 is the intercept and β_1 the slope of the regression line (both constants), and R_i the unexplained or residual variance.
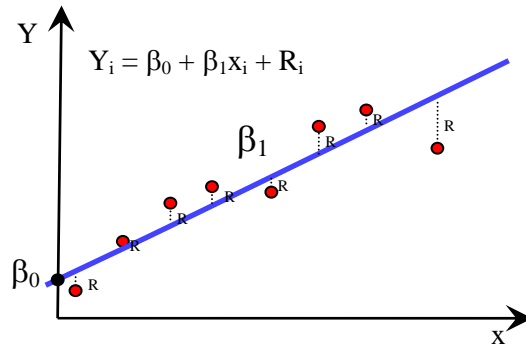

Figure A.1. The simple regression model.

For instance, if X represents time, and Y is skill level, then the regression model may show the acquisition of a skill by an individual over time. Alternatively, it could represent the progression of skill level related to age in a cross-sectional study (where every data point represents a value of a single individual).

In multiple regression, multiple predictor variables appear in the model, but its basic form remains the same:

$$Y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_i \ldots\ldots + \beta_n x_i + R_i \qquad (2)$$

Often research does not apply repeated measurements within one subject, or cross-sectional measurements with only one measurement per subject, but *repeated measurements within multiple subjects*. A problem arises when one deals with such nested, or 'multi-level' data sets. Figure A.2 shows such a data set (again, this is imaginary data) representing for instance developmental data from more than one child. A second subscript 'j' in the equation is now used to indicate the individual. For instance, Y_{23} refers to the value measured in the second measurement of the third subject. In this type of data set, one could determine the average developmental curve and note that variability increases with the value of x (as depicted by the line and shaded area). However, in this case it is ignored that

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measurements within individuals may be related. In particular, they are likely to be more related than measurements from different subjects. There may be consistent developmental pathways *within* individuals, but not *between* individuals. This type of information is lost when all measurements are treated as being equally (in)dependent.
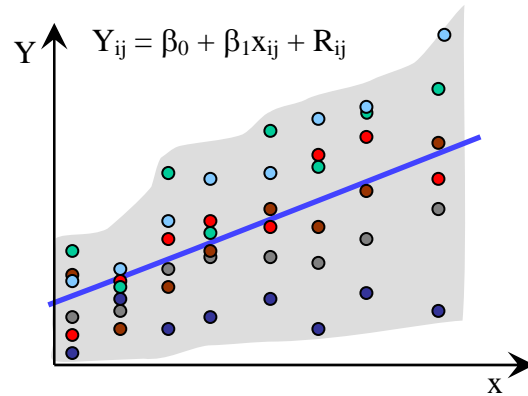

Figure A.2. Simple regression for multi-level data. Imaginary data from six individuals on eight measurement occasions. Different shades dots represent different individuals.

A more fundamental objection to using simple regression analysis with a hierarchical data structure is the violation of the test assumption of independent measurements that has strong implications for the chance of a type I error when testing significance. Barcikowski (1981) has shown that with an intra-subject correlation of only 0.05 in a design with 25 repeated measurements, the alpha level has inflated from 0.05 to 0.19. In other words, the test is too liberal.

If, on the other hand, a regression analysis is applied for each individual separately, it is ignored that although individuals may differ, there is probably substantial similarity in their behaviour. If each individual is considered separately, the information from other individuals is not taken into account in estimating the beta-coefficients for a specific subject, and chances of finding a significant effect are unnecessarily low: testing in this way is too conservative.

In multi-level regression analysis, the data set of Figure A.2 is modeled with a collection of regression lines (Fig. A.3). The basic regression equation reads:

$$Y_{ij} = \beta_{0j} + \beta_{1j}x_{ij} + R_{ij} \quad\quad\quad\quad\quad (3)$$
$$\beta_{0j} = \gamma_{00} + U_{0j} \quad\quad\quad\quad\quad\quad\quad (4)$$
$$\beta_{1j} = \gamma_{10} + U_{1j} \quad\quad\quad\quad\quad\quad\quad (5)$$

Note that the beta-coefficients are no longer constants, but vary between individuals. The multi-level nature of the data is thus reflected in the model. For each individual, a different regression line is modeled, with its own intercept and slope. Thus, the model consists of a collection of lines with an average intercept and an average slope (γ_{00} and γ_{10}) and individual deviances from those averages (U_0 and U_{1j}). Those individual deviances are the unexplained variance at the higher, between-individual, level. This distribution of the residual variance over the two levels is a unique feature of the multi-level regression equation. In figure A.4, the various components of the equation are graphically depicted.
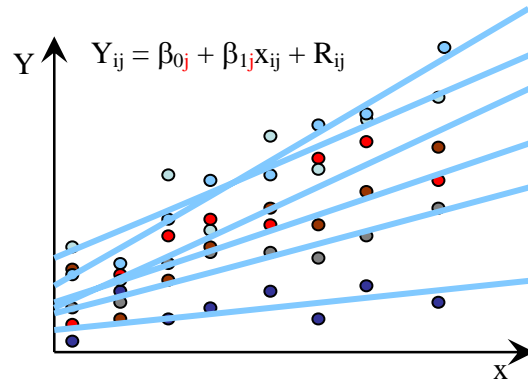

Figure A.3. The multi-level regression model. A separate regression line for each individual.

If X again represents time, and Y skill level, the model now represents the improvement of the skill over time in several individuals. It incorporates information about intra- and inter-individual development. The model allows testing of two types of questions: Does the research population improve significantly over time? Is there a significant difference between individuals with regard to their improvement?
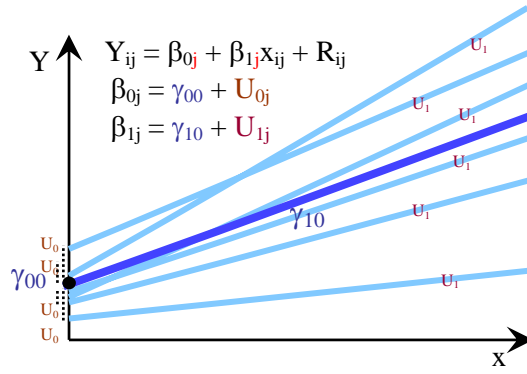
Figure A.4. The elements of the multi-level regression model: Average intercept (γ_{00}) and slope (γ_{10}) and individual deviations in intercept (U_0) and slope (U_1). The latter two make up the unexplained, or residual, variance at the higher level.

In addition to knowing *that* the effect of X on Y differs significantly between individuals, it is of course important to know *why*. Can a variable be identified that is associated with these inter-individual differences? For instance, are girls learning faster than boys? Are the smarter individuals progressing more quickly than the individuals that are less smart? Individual characteristics (higher-level variables) can be added to the model to explain part of the intercept and slope variation (Fig. A.5; values of Z are imaginary).

$$\beta_{0j} = \gamma_{00} + U_{0j} + \gamma_{01}Z_j \qquad\qquad (6)$$
$$\beta_{1j} = \gamma_{10} + U_{1j} + \gamma_{11}Z_j \qquad\qquad (7)$$

Variable Z represents some individual characteristic and γ_{01} and γ_{11} are the accompanying regression coefficients. Substituting equations (6) and (7) in equation (3) gives the following equation:

$$Y_{ij} = \gamma_{00} + \gamma_{10}x_{ij} + \gamma_{01}Z_j + \gamma_{11}Z_jx_{ij} + U_{0j} + U_{1j}x_{ij} + R_{ij} \qquad\qquad (8)$$

In this equation, the first part is called the 'fixed' part, and the last three terms are called the 'ramdom' part. The three regression coefficients following the average intercept are estimated to assess the main effects of variables X and Z, and the

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interaction-effect between X and Z respectively. Estimating the interaction effect indicates whether Z significantly influences the effect of X on Y. The term $U_{1j}x_{ij}$ is estimated to answer the question whether the effect of x on y differs significantly between individuals.
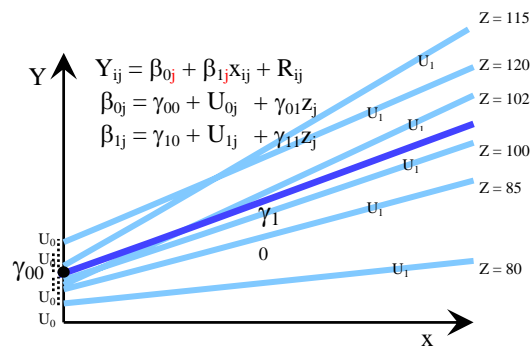

$$Y_{ij} = \beta_{0j} + \beta_{1j}x_{ij} + R_{ij}$$
$$\beta_{0j} = \gamma_{00} + U_{0j} + \gamma_{01}z_j$$
$$\beta_{1j} = \gamma_{10} + U_{1j} + \gamma_{11}z_j$$

Figure A.5. The multi-level regression model with both lower-level (x) and higher-level (z) explanatory (or predictor) variables.

For instance, if Z represents the IQ of a child, and X and Y are time and skill level, respectively, then the model can answer the question whether learning is faster when the IQ of a child is higher (Fig. A.5). Some examples of the "shape" of inter-individual variation in intra-individual change are given in Figure A.6.

Multi-level regression analysis is widely applicable. The model is also called the 'hierarchical linear model' but, in spite of its name, does not have to be linear. It can be polynomial, or built up from sections of lines (see Snijders & Bosker, 1999). The model can be made more complex by including multiple X and/or Z variables, or by defining a model with more than two levels.

The most common statistical tool for analysis of repeated measures data is a repeated measures analysis of variance (ANOVA). There is one main advantage of multi-level analysis over this method. Repeated measures ANOVA estimates regression coefficients inaccurately when data is unbalanced (unequal group sizes), in the case of missing data, and when only a few measurements are available per individual. Multi-level analysis uses the 'generalized least squares method', i.e. it uses data from other individuals to estimate the regression coefficients for a particular individual. This has been called 'borrowing strength'

or 'shrinkage to the mean', and makes it possible to test effects reliably in the aforementioned situations.

Multi-level data are not necessarily repeated measures data. It can also involve groups of subjects. The analysis of covariance method (ANCOVA) is often used when there are pre-existing groups, e.g. educational research using data from 30 children from 3 different classes. The difference with multi-level analysis is that the ANCOVA method cannot model characteristics of the higher-level unit (class). It can answer the question 'do units differ?' but not the question '*Why* do units differ?'. Furthermore, it neglects the original data structure by not correcting for intra-class correlation. And finally, a practical problem is that ANCOVA software cannot carry out the analysis on more than a few groups.
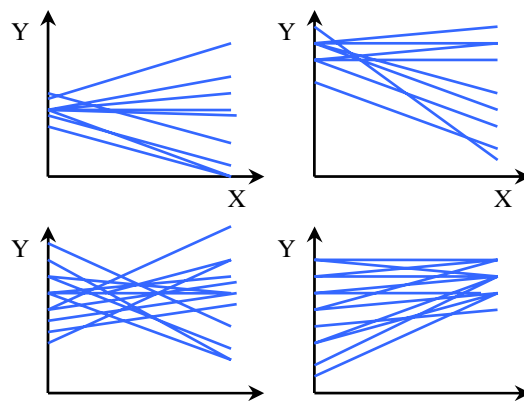

Figure A.6. Various depictions of inter-individual variability with regard to intra-individual change. In other words, various depictions of individuals who show "consistent, but different pathways" (Thelen & Smith, 1994).

Developmental and Learning Theory

With the availability of multi-level regression analysis, one may question the use of ANOVA as the default statistical method for developmental and learning studies. Theory on the process of development and learning has changed considerably over the last decades. Within the field of motor development, three

influential theories have renewed interest in the subject area that seemed dormant (Thelen, 1995). These theories are (i) the dynamic systems approach to development (Thelen & Smith, 1994), (ii) the constraints model for development formulated by Newell (1986) and (iii) the theory of neuronal group selection, popularly known as 'neural darwinism', developed by Edelman (1987).

The dynamic systems approach to development states that development is not programmed, but comes about through exploration and discovery (Thelen & Smith, 1994). The process of trying out different movement patterns and selecting the ones that 'work' is channeled by ecological constraints of the animal-environment system (Newell, 1986). For instance, an infant that learns to crawl on a wooden floor would be more likely to select a 'commando-style' crawl in which the arms propel the body forwards and the rest of the body is dragged over the floor than an infant that learns to crawl on carpet. The latter infant would be more likely to creep on all fours than crawl. In addition to the environment, the embodiment of the child is a major constraint. The anatomical characteristics of the human body are clearly linked to its functionality. The arms are for instance best suited for manipulation and the legs for support and locomotion. In children with physical handicaps that prevent parts of the body to perform their usual function, this function is often spontaneously picked up by different parts with an amazing ease. Children and adults, healthy and pathological, will always strive to perform optimally within the given set of constraints (Latash & Anson, 1996). In other words, the solutions that are discovered are by definition adaptive: usually they provide an optimal fit between the embodiment of the child, the task and the context. The dynamic or constraints-based view of motor development is supported by neurological data. It has been found that the neuronal connections in children are not genetically determined but to a large extent random with many redundant connections. In its most basic form, the theory of neuronal group selection states that on a neural level, experience-based selection takes place of functional connections over non-functional ones (Edelman, 1987).

Consequences of this view are that there is not one factor that causes motor development, and that the apparent existence of a design or master plan is only an illusion caused by the similarity of constraints within which we all grow up. The most important consequence of this view is that variability, both within and between individuals, is a meaningful characteristic of perceptual-motor development and deserves investigation in its own right. Thelen & Smith (1994) state:

'We encourage our readers to reach into their file cabinets where they store the studies they did not publish because their ANOVAs did not detect significant effects [..] Does the variability itself change over time? Are individual children variable between measures or are they pursuing consistent, but different pathways?' (Thelen & Smith, 1994, p.342)

The first question refers to intra-individual variability and can be studied by taking the variability of some measurement as dependent variable. Van Geert & Van Dijk (2002) have developed a number of methods for characterizing intra-individual variability in a time series. The second question refers to inter-individual variability in intra-individual change. This is precisely what the multi-level regression model aims to model (see equations 3, 4 and 5, Fig A.3) and therefore allows identifying. Moreover, it can point to relevant constraints of the developmental process by identifying co-variations between constraint levels and development (see equations 6, 7 and 8, Fig A.5).

Shifting the focus to the process of motor development (i.e. *how* instead of *what*) and therefore to intra-individual variability, not only has implications for the analysis of existing data. It also may determine future research designs. According to Thelen & Smith (1994) the new insights call for dense, longitudinal studies in a limited number of subjects. Multi-level analysis is particular suitable for this type of data, due to its use of the generalized least squares method. When acquiring such longitudinal data from newborns or infants, missing data or measurements at different points in time for different children is often a practical consequence of the design (e.g., Butcher, 2000). This type of data necessitates the use of multi-level regression analysis. Also, looking at the process of development, it may sometimes be informative to synchronize the longitudinal data from multiple subjects not on chronological age, but on a meaningful moment in 'developmental time', such as the onset of the growth spurt (Visser, 1998) or the appearance of a new skill (Van der Kamp et al., 1998; Wimmers et al., 1998). A posteriori aligning data to the occurrence of some unpredictable event artificially creates missing data at both ends of the time series. Again, due to the shrinkage or borrowing strength this is less of a problem for multi-level regression analysis than for ANOVA.

Samenvatting
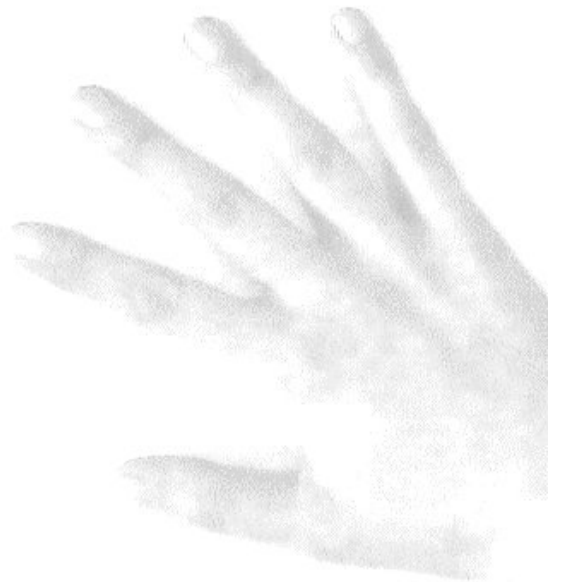
Beperkingen[1] van Coördinatie

Intrinsieke dynamica, gedragsinformatie en asymmetrie in bimanuele ritmische coördinatie

Dit proefschrift onderzoekt de rol die intrinsieke beperkingen (zoals handvoorkeur) en taak-gerelateerde beperkingen (zoals visuele feedback) spelen in de ritmische coördinatie van twee handen. Binnen de dynamische systeembenadering van bewegingssturing worden die beperkingen niet enkel gezien als factoren die de coördinatie beïnvloeden, maar als noodzakelijke voorwaarden bij het tot stand komen van motorische coördinatie. De beperkingen kanaliseren namelijk het proces van zelf-organisatie dat de coördinatie doet ontstaan. Ze sluiten coördinatie-mogelijkheden uit en sturen dus op een niet-deterministische manier de dynamica. Dit impliceert dat er niet een factor (bv. het centraal zenuwstelsel) is die coördinatie veroorzaakt, maar dat coördinatie ontstaat door de interactie van het zenuwstelsel met het lichaam en de omgeving. Om coördinatie te begrijpen, moet deze interactie worden begrepen.

In de natuur- en scheikunde zijn tal van voorbeelden bekend van spontane spatio-temporele organisatie in systemen bestaande uit vele interacterende elementen (zogenaamde complexe systemen), zoals het ontstaan van laserlicht en het onstaan van wervels in een verwarmde vloeistof. Het macroscopische patroon is in deze gevallen op geen enkele wijze "voorgeschreven" in de microscopie. Het uitgangspunt van de dynamische systeembenadering van bewegingssturing is dat motorische coördinatie ook gezien kan worden als een zelf-organiserend proces, gestuurd door beperkingen, zoals de elastische eigenschappen van het bewegingssysteem, de ervaring met bepaalde coördinatiepatronen, cerebrale asymmetrie en externe informatie over het uit te voeren coördinatiepatroon. Het doel van dit proefschrift is inzicht te geven in de interactie tussen die beperkingen door de analyse van stabiliteitskenmerken van coördinatie. In dit proefschrift is het

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[1] De Engelse term "constraint" kan vertaald worden met "beperking" of "selectievoorwaarde". De term is o.a. gebruikt door Kugler & Turvey (1980) in hun theoretische uiteenzetting van de dynamische systeembenadering van bewegingssturing, maar wordt tegenwoordig voornamelijk gerelateerd aan het model van "constraints" van Newell (1986).

tweehandig ritmisch tikken onderzocht. Deze eenvoudige coördinatie-taak is gebruikt omdat is gebleken dat het een goede manier is om algemene eigenschappen van coördinatie te bestuderen.

Hoofdstuk 2 beschrijft een studie naar de invloed van muzikale ervaring en zogenaamde "gedragsinformatie" op ritmische coördinatie. Tien proefpersonen met en tien proefpersonen zonder muzikale ervaring tikten een in-fase patroon (de 2 vingers tikken precies tegelijkertijd), een anti-fasepatroon (precies tegengesteld) en een 90°-uit-fase patroon (ongelijk, de ene tikt iets eerder dan de ander) in een ritmische tiktaak. Een metronoom gaf aan het begin van elke trial het tempo en ritme aan. De proefpersonen werden verzocht met de metronoom mee te tikken en zo constant mogelijk door te gaan met tikken wanneer de metronoom ophield. Een visueel signaal halverwege elke trial gaf aan dat de proefpersonen naar een ander patroon moesten overschakelen. De patronen werden eerst op een abstracte manier aangeboden ("tik precies om en om") en toen op een ecologisch relevante manier ("stel je voor dat je wijsvingers de voorbenen van een dravend paard zijn"). In de ecologische conditie werden de drie patronen aangeduid als stap, draf en galop. De proefpersonen met muzikale ervaring bleken een stabielere coördinatie te laten zien dan de proefpersonen zonder muzikale ervaring. Muzikale ervaring liet geen interactie zien met de aangeboden informatie over de patronen. Die informatie had echter wel een verschillende invloed op de coördinatie-patronen. Het in-fase patroon werd minder stabiel uitgevoerd in de ecologische conditie, terwijl de andere twee patronen stabieler werden uitgevoerd. Een soortgelijke interactie werd gevonden voor de verschillende wisselcondities.

Daarnaast lieten de proefpersonen een sterke inter- en intra-individuele voorkeur zien voor een van de twee typen galop (linksleidend of rechtsleidend) en voor een type strategie om van een patroon naar een ander patroon over te schakelen. Die twee keuzen bleken sterk aan elkaar gerelateerd. Dit suggereert een asymmetrie in de coördinatie, die mogelijkerwijs kan worden toegeschreven aan cerebrale dominantie, oftewel handvoorkeur. Echter, de data kan hierover geen uitsluitsel geven, ondermeer omdat slechts twee linkshandige proefpersonen deelnamen aan het experiment.

Het experiment dat besproken wordt in *hoofdstuk 3* richt zich expliciet op de interactie tussen intrinsieke asymmetrie (handvoorkeur) en taak-gerelateerde asymmetrie. Elf linkshandige en dertien rechtshandige jonge volwassenen werden

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vergeleken met betrekking tot de uitvoering van het asymmetrische galoppatroon (90° uit fase), zowel in de linksleidende als de rechtsleidende variant. Ter vergelijking werd ook het anti-fase patroon getikt. De tiktaak was evenals in hoofdstuk 2 een continueringstaak, maar in dit geval kregen de proefpersonen de instructie gedurende de hele trial zo constant mogelijk hetzelfde patroon te tikken. Eerder onderzoek heeft laten zien dat in multi-frequentie taken (waarbij de ene hand bijvoorbeeld twee keer zo snel tikt als de andere) de handen twee verschillende hand-rollen aannemen. De snelle hand functioneert als "maatgever" terwijl de langzame hand op zo'n manier tikken "invoegt" dat het gevraagde coördinatiepatroon ontstaat. In multi-frequentie taken is de coördinatie beduidend beter wanneer de voorkeurshand snel tikt en de niet-voorkeurshand langzaam dan vice versa. Het is echter niet duidelijk of dit het gevolg is van de asymmetrie in handrol of de asymmetrie in snelheid. In het galoppatroon is de snelheid van beide handen gelijk en is er alleen een asymmetrie op het niveau van de koppeling. Daardoor biedt het galoppatroon de mogelijkheid de hypothese te testen dat de kwaliteit van coördinatie samenhangt met de verdeling van de handrollen over de twee handen. Naast de symmetrie van het fasepatroon werd ook de symmetrie van de visuele feedback gemanipuleerd, omdat eerder onderzoek heeft uitgewezen dat asymmetrische feedback het effect van intrinsieke asymmetrie kan versterken.

De resultaten bevestigden de hypothese dat het gallop-patroon, net als de multi-frequentie patronen wordt gekenmerkt door twee verschillende handrollen. Zo'n asymmetrie werd niet gevonden voor het anti-fase patroon. De hand die een kwart cyclus voorliep had een sterkere invloed op de hand die volgde dan vice versa. Bovendien waren de intervallen tussen twee opeenvolgende tikken stabieler in de hand die voorliep dan in de volghand. Er werd geen interactie met handvoorkeur gevonden, d.w.z. de coördinatie verslechterde niet wanneer de niet-voorkeurshand de leidende rol aannam. Dit suggereert dat de verslechtering in de multi-frequentie taken te maken zou kunnen hebben met het verschil in frequentie. Het galoppatroon laat zien dat "handigheid" (d.i. welke hand het meest bekwaam is) in twee-handige coördinatie taak-afhankelijk is.

In *hoofdstuk 4* wordt hetzelfde paradigma als in hoofdstuk 3 gebruikt om de interactie tussen intrinsieke asymmetrie, veroorzaakt door ziekte, en taak-asymmetrie te onderzoeken. Mensen met de ziekte van Parkinson hebben problemen met tweehandige coördinatie. Het is echter niet duidelijk wat de oorzaak van deze problemen is. Het onderzoek naar coördinatie-problemen heeft

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zich voornamelijk gericht op personen met mild Parkinsonisme. Met name in deze groep zijn de symptomen, zoals rigiditeit en tremor, vaak ongelijk verdeeld over de linker- en rechterlichaamshelft. Het is aannemelijk dat de coördinatie dynamica tussen de ledematen hierdoor is veranderd. De vraag die wordt onderzocht in dit hoofdstuk is of de coördinatie-problemen die Parkinsonpatiënten ondervinden een direct gevolg zijn van het onvermogen de ledematen te koppelen of (gedeeltelijk) een gevolg zijn van de asymmetrische biomechanische veranderingen in de ledematen. Een groep Parkinsonpatiënten (premorbide rechtshandig, 37-89 jaar) is onderzocht, waarvan een deel symmetrisch was aangedaan (*N*=10), een deel voornamelijk links was aangedaan (*N*=10) en een deel voornamelijk rechts was aangedaan (*N*=10). Een op leeftijd en geslacht gematchte gezonde controlegroep (*N*=30) is ook meegenomen in het onderzoek. Deze controlegroep leek minder flexibel in het aannemen van verschillende handrollen, afhankelijk van de taak, dan de jonge volwassenen in het vorige onderzoek (zie hoofdstuk 3). Gegevens van de Parkinsonpatiënten boden weinig ondersteuning voor de hypothese dat biomechanische asymmetrie de coördinatieproblemen veroorzaakt, maar ondersteunen het idee dat de koppeling tussen de ledematen is veranderd, ofschoon niet volledig in lijn met het voorgestelde model. Premorbide handvoorkeur bleek een belangrijke intrinsieke beperking van de beschikbare koppelingsstrategieën.

In *hoofdstuk 5* worden tenslotte de bevindingen geëvalueerd en besproken met de nadruk op hun betekenis in het bredere programma van de dynamische systeembenadering van motorische coördinatie. Binnen deze benadering is tot voor kort relatief weinig aandacht geweest voor onderzoek naar het effect van cognitieve factoren op de coördinatie dynamica, mogelijkerwijs vanwege de paradoxale aard van zo'n onderneming. Het belang van asymmetrie is daarentegen herhaaldelijk benadrukt. Het verbreken van de symmetrie verschaft een mechanisme voor de controle van bewegingen. De resultaten van de hierboven beschreven studies suggereren echter dat asymmetrie ook gepaard kan gaan met een beperking van de coordinatie-mogelijkheden.

Daarnaast wordt de positie van de dynamische systeembenadering binnen het veld van bewegingssturing besproken. Vanuit wetenschapsfilosofisch oogpunt vormt de dynamische systeembenadering een sterk onderzoeksprogramma. De benadering is echter (nog?) niet algemeen geaccepteerd en staat tegenwoordig tegenover een tendens naar materialistisch reductionisme in de studie van het

menselijk gedrag. Vervolgens wordt ingegaan op de dynamische systeem-benadering van leren en her-leren (revalidatie) en de rol van de leraar of therapeut in dit proces. Tenslotte wordt beargumenteerd dat toekomstig onderzoek zich meer zou moeten richten op de coördinatie van bewegingen waarbij meerdere vrijheidsgraden een rol spelen.

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en enige woorden
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About the author

Martine Verheul was born in Breukelen on the 29th of July, 1974. She studied Human Movement Sciences at the Vrije Universiteit in Amsterdam between 1992 and 1997. For her MSc degree, she did research projects at the academic hospital of the Vrije Universiteit with Richard van Emmerik and Robert Wagenaar (trunk rotation while walking in adults with and without Parkinson's disease) and at the Montreal Rehabilitation Institute with Mindy Levin and Anatol Feldman (stretch reflex threshold regulation in stroke patients). In the final year of her studies, she obtained the certificate in higher healthcare education. Her subsequent PhD project at the University of Groningen has resulted in this thesis. During her PhD appointment, she was guest lecturer on the dynamic systems approach to motor control at the Technical College Amsterdam ("Mensendieck" Remedial Therapy School) and at the University of Maastricht (Department of Psychology), and illustrated a textbook in behavioural neurology. She presented her research findings at national and international conferences. At home ground, she won the Poster Award 2000 of the Graduate School for Behavioral and Cognitive Neurosciences. Martine is currently working as a post-doctoral research fellow at the Institute for Biophysical and Clinical Research into Human Movement (IRM) of the Manchester Metropolitan University. She investigates the development of perceptual-motor coordination in primary school children. In addition, she teaches courses on motor control, skill acquisition and motor development.

Over de auteur

Martine Verheul werd geboren in Breukelen op 29 juli 1974. Tussen 1992 en 1997 studeerde ze bewegingswetenschappen aan de Vrije Universiteit in Amsterdam. In die tijd deed ze onder andere een onderzoeksstage in het VU ziekenhuis bij Richard van Emmerik en Robert Wagenaar (romprotatie tijdens het lopen bij volwassenen met en zonder de ziekte van Parkinson) en in het *Institute de Réadaptation de Montréal / Montreal Rehabilitation Institute* met Mindy Levin en Anatol Feldman (regulatie van de rekreflex drempelwaarde bij mensen met een halfzijdige verlamming ten gevolge van een hersenbloeding of -infarct). In het laatste jaar heeft zij ook de opleiding gevolgd tot docent in het hogere gezondheidszorg onderwijs. Het daaropvolgende promotie-onderzoek aan de Universiteit van Groningen heeft geresulteerd in dit proefschrift. Tijdens haar aanstelling als onderzoeker in opleiding heeft Martine gastcolleges gegeven over de dynamische systeem benadering van bewegingssturing bij de opleiding Oefentherapie Mensendieck aan de Hogeschool van Amsterdam en bij de faculteit Psychologie van de Universiteit van Maastricht, en illustreerde ze een leerboek gedragsneurologie. Ze heeft haar onderzoeksbevindingen gepresenteerd op nationale en internationale congressen. Op Nederlands terrein won ze de posterprijs 2000 van de onderzoekschool *Behavioral and Cognitive Neurosciences*. Momenteel werkt Martine als post-doctoraal onderzoeker bij het *Institute for Biophysical and Clinical Research into Human Movement* (Instituut voor biofysisch en klinisch onderzoek naar menselijk bewegen) aan de *Manchester Metropolitan University*. Ze onderzoekt de perceptueel-motorische ontwikkeling van kinderen in de basisschoolleeftijd. Daarnaast geeft ze onderwijs over bewegingssturing, motorisch leren en motorische ontwikkeling.

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