INTRODUCTION

We are frequently confronted with situations in which we have to skillfully coordinate our hands to solve a particular motor task. Tying shoelaces, opening a bottle of water, or unbuttoning a shirt are just three examples of such bimanual tasks. Most of the time, we do not have to spend much effort to produce these manipulative actions that become important in the daily interaction with our environment. The precise way in which we engage our two upper limbs in the production of voluntary actions is thereby a unique feature to the human species and must be seen as a hallmark in evolution. With practice, even the most complex motor patterns can be learned, enabling us to master such tasks as playing the piano, juggling five or more balls up in the air, and communicating through sign language.

An interesting observation is the fact that in most of these task the two hands do different things at the same time in order to satisfy a particular action goal - like drinking out of a bottle. Thereby, it is often necessary to execute a number of smaller action sequences. In the example 'drinking out of a bottle' we have to open the bottle first before we can drink out of it. In the opening phase, this requires to hold the bottle with one hand while unscrewing the lid with the other hand. Quiet contrary, in the drinking phase, the same hand that just held the bottle steady now translates it to the mouth, while the other previously active hand holds the lid. This procedure is then reversed when we want to screw the lid onto the bottle again. Such distinct behavior can also be seen as good evidence for the often observable role-assignment between the two hands (Guiard, 1987), where functional differences arise relative to the particular action goal. From this perspective, the relationship of the different hand actions only becomes apparent under the light of the external goal of these actions (Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004).

Although we perform most tasks effortless and with great ease, some limitations can become obvious whenever we have to execute bimanual actions with high temporal and/or high spatial precision requirements. Polyrhythmic tapping and trying to put a thread through a needle are two examples. Performance failures and action slips are frequently observed under these conditions. We experience great difficulty in producing a difficult tapping rhythm (e.g., 4:5) or we fail to keep our hands steady and are thus, unable to put the thread through the needle. Given these observations, questions about the nature of limitations in task performance arise.

The study of such complex manual behavior involving multiple effector systems has provided a window into exploring the processes underlying human action control. Research

on bimanual coordination produced a vast amount of experimental data in support of limitations in the temporal as well as in the spatial domain (Ivry et al., 2004; Mechsner, 2004; Swinnen, 2002, Swinnen & Carson, 2002). After a short excursion into research on unimanual control[1], the following chapter on the Review of Literature will then discuss some of these limitations further and introduce the standard paradigms that have been used to study bimanual movement control. Here, two theoretical approaches to explain the observed coupling phenomena in bimanual coordination will be contrasted. The motor coordination approach focuses on movement-intrinsic properties, whereas, the target coordination approach emphasizes the important role of movement targets and external action goals. Studies in favor of either one of these two approaches will be briefly presented to sketch out the current debate on (bimanual) action control. In the end, the rationale for the present study will be outlined and a new paradigm is introduced.

[1] Despite the fact that this dissertation is on bimanual coordination, I feel that it is important to also take a brief look at some of the early research on unimanual coordination. Two reasons motivate such an excursion: 1. Early concepts about the processes underlying unimanual movement control, such as movement programming, directly influenced some of the theoretical approaches to explain bimanual movement control afterwards. 2. Paradigms that had been used to investigate unimanual movements before, were often extended to bimanual situations. Prime examples are the studies by Heuer, Spijkers and colleagues (e.g., Heuer et al., 1998; Spijkers et al., 1997), who used Rosenbaum's precuing task (1980) to examine movement parameters that contribute to spatial interference observed in bimanual coordination.

CHAPTER I - REVIEW OF LITERATURE

Setting the Stage: Research on Unimanual Movement Control

Before the simultaneous coordination of our two upper limbs became the focus of intense research in the fields of Experimental Psychology and Motor Behavior, researchers investigated the control of single limb movements. Here, the works of Woodworth (1899), Hollingworth (1909), and Thorndike (1914) must be mentioned, because they represent the earliest systematic contributions about the processes involved in human skill learning and movement control. Even today, Woodworth's (1899) paper on *The Accuracy of Voluntary Movement* is still one of the most cited papers in the motor behavior literature. His research on rapid arm and hand movements was motivated by his view that aiming movements comprise a two-stage process, the *initial-impulse* and the *current-control* phase. By this definition, Woodworth already foreshadowed the main ingredients of theories that half a century later tried to tie processes such as movement preparation, movement execution and feedback control together (e.g., Anochin, 1967; Schmidt, 1975).

These later theories were then greatly influenced by the information-processing approach to investigate the human cognitive capacities in the field of experimental psychology – especially influential at that time was the book by Neisser (1967) called *Cognitive Psychology*. According to the information-processing approach, some features of a particular task have to be processed in order for the task to be successfully completed. From this, pertinent questions arise: *What are these features and how are they processed? What are the limitations of processing? For the sake of task repetition, are at least some aspects of these features stored? And if so, what is the medium and the format for storage?*

For the control of human movement, information processing meant that various motor parameters, such as the direction or the amplitude of a movement, have to be specified before the action can be carried out (Keele, 1968; Kerr, 1978; Rosenbaum, 1980). Once these parameter values are defined, they are then fitted into a motor program, which can be seen as a form of "central representation" (Schmidt, 1982, p. 38). Early concepts of such central representations that gave rise to the idea of motor programs came from Henry and Rogers (1960), Pew (1966), and Posner (1967). In an influential article published in 1968, Keele defined the motor program as *"a set of muscle commands that are structured before a movement sequence begins, and that allows for the entire sequence to be carried out uninfluenced by peripheral feedback"* (Keele, 1968, p. 387). Motor programs must contain

specific information about the movement before its initiation in order to shape its outcome (Adams, 1971; Keele, 1968), but the motor program must also be updated by peripheral feedback about the ongoing processes (Anochin, 1967; Schmidt, 1975). Schmidt's concept of a closed-loop control system (1975) allows for the constant update of the motor program about the ongoing activities through peripheral feedback. Depending on this feedback, the motor program is subject to constant change and re-adjustment.

Complex movements that share a unique pattern of activity are thought to be stored within a particular class of movements in memory (Shapiro & Schmidt, 1982; Schmidt, 1982). To avoid a presumable storage problem for an infinite number of movements, similar actions are organized in the format of generalized motor programs (GMP). Thereby, each GMP can include very different actions. For instance, throwing a baseball, serving a tennis ball, or performing an overhand volley may be classified within the very same GMP, because they share the same *invariant* features, such as the order of events, the relative timing, and the relative force output (Schmidt & Lee, 1999). However, these actions are quite different and the question arises: How can these complex actions be accomplished? The seemingly trivial answer is through defining their *variant* features (Schmidt, 1985), such as the muscles selected, the overall duration of an action, and the overall force output (Schmidt & Lee, 1999). However, as we know from our own experience, performing some of these skills is often not trivial at all, and that it can take much effort and even more time to practice in order to "define" these *variant* features.

The key motor parameters that are now widely believed to be the candidates for pre-specification during motor programming have been systematically investigated for unimanual reaching movements in the works of Rosenbaum (Rosenbaum, 1980; Rosenbaum, Barnes, Slotta, 1988; Rosenbaum & Kornblum, 1982). His influential paper on the *Human Movement Initiation: Specification of Arm, Direction, and Extend*, Rosenbaum (1980) provides an experimental method to single out the relative contributions of different parameters and their values along different dimensions on the planning of discrete movement responses. In his experiments, participants were asked to perform discrete movements either with their right or left arm, over short or long amplitudes, and in forward or backward direction. To specify the forthcoming movements (e.g., left arm, short amplitude, forward), Rosenbaum used movement precueing in a reaction time (RT) task, where symbolic cues provided information about none, some, or all of the defining values of the action. The logic of the precueing technique is that after subtraction from a full set of precues, the other RT values must reflect the time it takes to specify those values that are not precued. The results showed that all of

these variables are specified before a movement can be executed – with the longest RTs for arm, shorter RTs for direction, and shortest RTs for extend. In the conclusion, Rosenbaum proposed a model of value specification that is consistent with the distinctive-feature view of motor programming (Chomsky, 1965). Characteristic for the distinctive-feature view is, that parameter values can be independently specified along a common dimension, without necessarily affecting other parameters on differing dimensions. This allows for an efficient modification of the motor program, as only selective parts of it can be adjusted at a time.

Moving on: Research on Bimanual Coordination

After methods to investigate unimanual movement control had been established, research on the control of bimanual movements followed in close succession (Cohen, 1971; Corcos, 1984; Kelso, Southard, & Goodman, 1979; Kelso, Putnam, & Goodman, 1983). These studies often extended existing paradigms that had been used to study unimanual coordination before, to bimanual situations. It became apparent that when both hands move simultaneously, strong coupling effects arise such that neither of the hands is able to perform independent actions. These interdependencies of the two hands can be observed in both the temporal and spatial domain. Coupling effects in the temporal domain were reported in an early study by Kelso, Southard, and Goodman (1979). These authors asked the question: How will subjects perform under situations in which they have to perform simultaneous movements of the two hands to targets of widely disparate difficulty? A paradigm to study this question experimentally had been provided by Fitts before, which became known as Fitts' task (Fitts, 1954, Fitts & Peterson, 1964). In Fitts' task, participants move a stylus alternately between two targets. Under different conditions, the distance between the targets and their width is systematically varied. Fitt' law (Fitts, 1954; Fitts & Peterson, 1964) predicts that performance in such a task (e.g., movement time, error rate) will depend on the ratio of movement amplitude and precision requirements. In their bimanual version of Fitts' task, Kelso et al. (1979) found that participants initiated and terminated their movements simultaneously - independent of whether the two hands had to perform actions of similar or disparate difficulty. Even for actions of disparate difficulty, kinematical analyses of the movement trajectories revealed almost perfect synchrony between the peaks in the velocity-time and acceleration-time curves for the two hands (Kelso et al., 1979; Kelso et al., 1983). These findings were first evidence for the observation that the simultaneous performance of two manual tasks results in a tight temporal coupling of the limbs.

Coupling effects in the spatial domain were demonstrated by Franz, Zelaznik, and McCabe (1991). These authors asked participants to continuously draw circles and lines, either single-handed, one task at a time or bimanually, for a 20 seconds period per trial (see Figure 1). When compared to the single-handed task, drawing bimanual circles and bimanual lines did not change the spatial topology of either form. In contrast, under conditions in which participants were asked to produce two movements of different spatial form (e.g., a line with one hand and a circle with the other hand), they exhibited spatial accommodation in the performance of both tasks. That is, a mutual assimilation in the spatial topology of each shape was obtained, resulting in elliptical figures. This assimilation of shapes occurred despite a tight temporal coupling between the two hands, providing strong evidence for the existence of spatial constraints governing bimanual movement coordination.

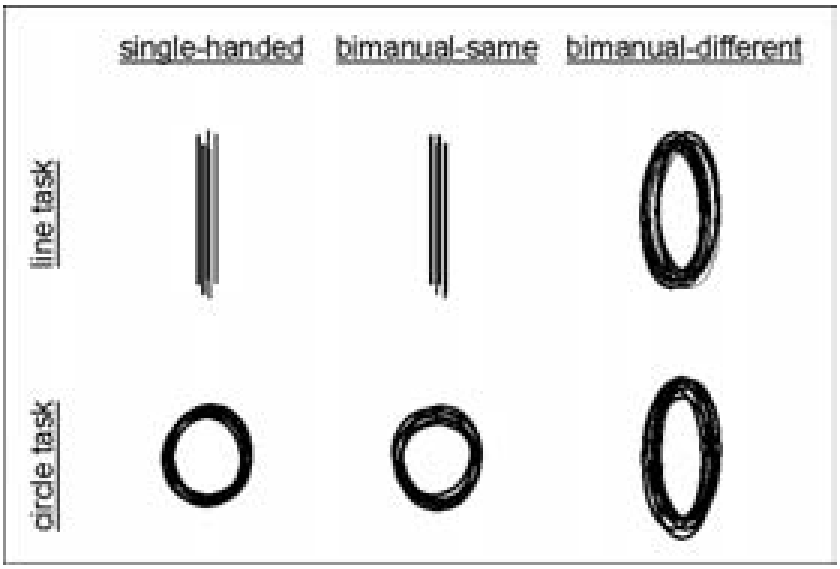

Figure 1. Depicted is the line-and-circle drawing task by Franz, Zelaznik, & McCabe (1991). In this task, participants were asked to draw circles and lines, either single-handed or bimanually. Results showed strong spatial assimilation of the two forms under condition in which the two bimanual tasks differed.

The Motor Coordination Approach

To account for such coupling effects, most researchers have drawn on coordination at the motor level. For example, Cohen (1971) and Kelso (1984) attributed spatio-temporal coupling effects in periodic, bimanual movements to a tendency towards co-activating homologous muscles. In Kelso's (1984) index-finger oscillation task, participants had to oscillate the index finger of their left and right hand towards and away from the body midline to the beat of a metronome (see Figure 2). Two modes of instruction were possible: In the in-phase mode, participants performed mirror-symmetrical finger movements, which can be

described by a spatio-temporal phase relationship of $\phi = 0°$. In the anti-phase mode, participants performed parallel finger movements, which can be described by a spatio-temporal phase relationship of $\phi = 180°$. When the pace of the metronome was sped up, distinct switches from the parallel to the mirror-symmetrical movement pattern were frequently observed, but not vice versa. This behavior has become known as phase shifting, and has been put into mathematical terms in the so-called HAKEN-KELSO-BUNZ Model (Haken, Kelso, & Bunz, 1985). Together, the landmark study by Kelso and the HAKEN-KELSO-BUNZ Model provided the basis for the dynamical systems theory of motor control (Kelso, 1995; Schöner & Kelso, 1988; see also Turvey, 1990).

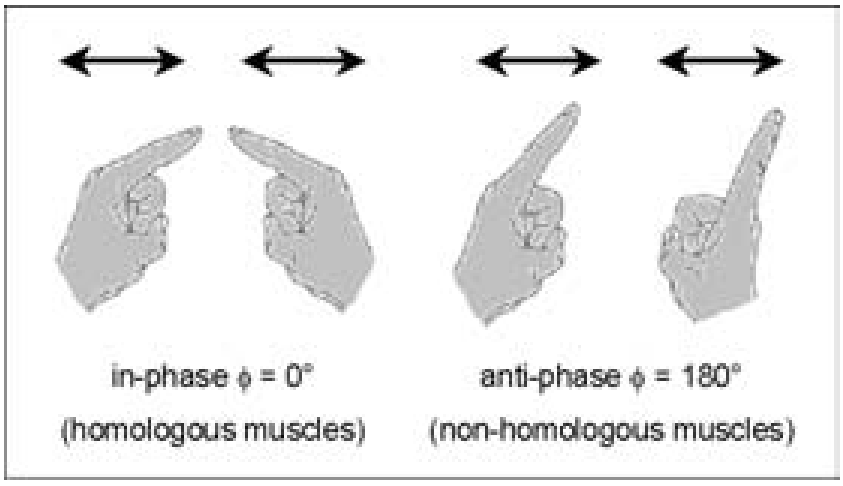

Figure 2. Depicted is the classic bimanual index-finger oscillation task by Kelso (1984). Here, participants oscillate the index finger of their left and right hand towards and away from the body midline - forming mirror-symmetrical (homologous muscles) and parallel (non-homologous muscles) movement patterns. With higher oscillation frequencies, the mirror-symmetrical pattern is more stable than the parallel pattern (adopted from Swinnen, *Nature Review Neuroscience*, 2002).

The tendency for mirror-symmetrical movement patterns has been observed in a number of other bimanual tasks, such as four-finger tapping (Kelso, 1995), bimanual circling (Carson, Thomas, Summers, Walters, & Semjen, 1997; Semjen, Summers, & Cattaert, 1995), and forearm rotation (Byblow, Carson, Goodman, 1994; Carson, Byblow, Abernethy, & Summers, 1996; Carson, Riek, Smethurst, Parraga, & Byblow, 2000). The observation of mirror-symmetry over a variety of tasks has led researchers to speculate about the relative roles of homologous muscles, efferent muscle commands, and the organization of the central nervous system on the control of human movements (for an overview see Swinnen, 2002). In this regard, it has been proposed that periodic movements of the two hands should be biased towards symmetrical patterns due to the symmetrical organization of the neuromuscular-

skeletal system driving them (Carson, 1996; Carson et al., 2000, Cattaert, Semjen, & Summers, 1999).[2]

Spatial coupling effects have been associated with preparatory processes during motor programming and the specification of particular kinematical parameters, such as movement amplitude and/or direction (Corcos, 1984; Heuer, 1993; Marteniuk, MacKenzie, & Baba, 1984; Sherwood, 1994). According to this account the specification of two unequal parameter values for the two hands generates programming interference, thereby demanding higher planning costs than the specification of two equal parameter values. As a result, when unequal parameter values are specified for the two hands, movement initiation times are longer as compared to situations in which the parameter values are equal. This notion has been supported for amplitude (Heuer, Spijkers, Kleinsorge, van der Loo, & Steglich, 1998; Spijkers & Heuer, 1995; Spijkers, Heuer, Kleinsorge, & van der Loo, 1997), as well as direction (Steglich, 2002). Further, the amount of the interference effect may depend on time constraints. If interference is due to neuronal cross-talk between the two hemisphere/hand systems during the specification of movement parameters, it may be stronger under conditions when the cue calls for an immediate response (Cardoso de Oliviera, 2002; Franz, Eliassen, Ivry, & Gazzaniga, 1996) as compared to conditions when there is sufficient time for the specification process to take place (Heuer et al., 1998; Spijkers et al., 1997).

The factors influencing the spatial coordination of bimanual actions have been extensively studied by Heuer, Spijkers, and colleagues (Heuer, 1993; Heuer et al., 1998; Spijkers & Heuer, 1995; Spijkers et al., 1997). In their standard paradigm (e.g., Spijkers et al., 1997), participants are asked to perform reversal movements into the fronto-lateral direction over the same or different amplitudes, 10 and 20 cm long, respectively. In each trial, the German words for “short” and “long” (“kurz” and “lang”) specified the required amplitudes for the left and right hand separately. For example, if the two words “short” and “short” appeared on the screen, participants simultaneously performed a movement over 10 cm with their left hand and a movement over 10 cm with their right hand. However, if the two words “short” and “long” appeared on the screen, participants simultaneously performed a movement over 10 cm with their left hand and a movement over 20 cm with their right hand. The results of Spijkers et al. (1997) showed that participants initiated their movements faster under conditions in which the same amplitude was required for the two hands, as compared to

[2] Here, it should be noted that the tendency for symmetric movements is not only confined to egocentric space (the preference of moving in mirror-symmetry involving the co-activation of homologous muscles groups of similar limbs), but can also be found with reference to allocentric space (the preference of moving two different limbs in the same direction) (Swinnen et al., 1997), and even between two people (Schmidt et al., 1990).

conditions of different amplitudes. The authors explained these findings with interference that arises as a result of neuronal cross-talk during motor programming when different parameter values have to be specified for the two hands (Marteniuk et al., 1984; Spijkers & Heuer, 1995). Thus, the spatial coupling effects observed in bimanual coordination depend upon concurrent parameter specification processes between the two limbs (Heuer, 1993). From this perspective, specifying similar parameter values for the two hands should always enhance coordination, whereas specifying different parameter values should hamper coordination.

Another finding of the Spijkers et al. study (1997) was that cross-talk found in discrete bimanual tasks is exhaustive. The authors used movement precueing (Rosenbaum, 1980) to specify the amplitudes for each hand. Upon a go signal, following at variable intervals after the cue presentation (e.g., 0, 125, 250, 375, 500, 750, and 1000 ms, Experiment 2), participants initiated their movement responses. The authors assumed that participants would not initiate their movements before the specification process was finished. Thus, reaction time (RT) should be a sensitive measure for the amount of interference. Their results showed that the RT for movements over the same and different amplitudes declined as a function of the precueing interval, with the differences between the two movements diminished at the longest interval. According to these results, movements over different amplitudes can be prepared equally well when there is sufficient time provided for the specification processes to take place. These findings are consistent with the notion of transient effector coupling during the programming of bimanual movements, which is predicted by the transient coupling hypothesis (Heuer, 1993). With regard, the transient coupling hypothesis states that different amplitudes can be programmed concurrently, although, more time is need for the programming of different parameter values. However, when there is sufficient time for the programming to take place, asymmetry effects in movement preparation diminish (Heuer et al., 1998; Spijkers et al., 1997).

The Action Goal- and Target-Coordination Approach

The research discussed so far focused mainly on the motor level and thus, on movement-*intrinsic* properties to explain bimanual action coordination. Such an approach, however, appears to be counterintuitive when looking at the way of how we normally interact with our environment. That is, we do not move for the sake of moving, but we act to modify our body-*extrinsic* environment in a specific way. We reach out to grasp a bottle, push down the handle to open a door, turn the switch to turn on the light, dial a number to make a phone