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Coordination of Unimanual Continuous Movements with External Events

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Coordination of Unimanual Continuous Movements with External Events

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DISSERTATION

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Contents

Chapter 1

General Introduction

Everyday life requires us to coordinate our own movements with our environment. Imagine pushing a shopping cart through the supermarket. You will be constantly controlling your speed and direction to avoid collisions with other shoppers or shelves. Other shoppers moving at their own speed will not make your task easier. Nevertheless, it is an action we perform seemingly effortlessly countless times in our lives. What we consciously experience in those situations is the will to move, to grab, to act, but we are unaware of the complex operations performed by our nervous sytem to generate the commands to make the right muscles flex. Even a simple grasping movement requires spatial coordinates of the object to be translated into motor commands which bring the hand to the intended position. Quite complex calculations have to be completed by the central nervous system (CNS) to do this; however, the transformations we are going to deal with in this dissertation will take us even one step further. In addition to coordination demands, many tasks introduce transformations between the actual movement and the intended effect. For example: an activity most of us perform regularly is the use of a computer mouse. Here the transformation acts between the hand movement and the movement of the cursor (which is the intended effect). The hand moves on the table but the visual effect is presented on the screen. Hand movements away from the body are translated into upwards movements on the screen and movements towards the body into downwards movements. If you ever tried to move your mouse with the hand you do not usually use for this, maybe because the other one was busy holding your mobile/sandwich/cup, you may have noticed that the task of moving the cursor somewhere is not as trivial as it presents itself in everyday use.

It is important to understand how our motor system and perceptual system interact and deal with such transformations, which at a closer look are nowadays omnipresent. We can hardly spend an hour without performing an action where the goal is not the movements of our own hands but the effects they produce in the environment, often via a wide range of tools and devices. Human tool use goes back about 2.4 million years and since that time we have learned to adapt to transformations that enable us to produce changes in the environment that our bare hands could not bring forth. Since the tools we use nowadays have become a bit more complex than the common prehistoric hand axe, it is important to design them and the interfaces via which they are controlled in a way to minimize errors.

A large amount of studies have been done on the subject of voluntary motor control. Research on the basics of motor coordination of the upper limbs may be divided into two lines of research, unimanual and bimanual research, which have both influenced the study which will be presented in the following.

Unimanual research, which focuses on the time course of coordinative actions and the determination of features and constraints of motor programs, often employs discrete movements which are not likely to represent everyday actions but allow access to basic coordination mechanisms. Everyday coordinative actions are of course not easy to study under controlled conditions. They mostly involve both of our hands and are of enormous complexity. Theoretical and technical progress allowed have bimanual coordination research to evolve. Here strong spatial and temporal coupling patterns became obvious when the two hands move simultaneously.

1.1 Motor Coordination

In order to generate a movement, the nervous system has to solve three main problems: First, it has to localize the target in external space or Where do I want to go? Second, to analyze the current state of the motor system or Where am I? Third, it has to define a hand trajectory or How do I best get from here to there? There are several divergent models on how this may be accomplished, each of which is supported and contradicted by solid experimental evidence (for a review see Desmurget, Pelisson, Rossetti, & Prablanc, 1998). The diversity of opinions on the implementation of motor control indicates that the nervous system might be able to use different strategies, depending on the task at hand. Desmurget et al. (1998) therefore call for studies that systematically test the effect of environmental constraints and compare these in different experimental situations. The present study will try to comply with this request by studying how perception and action interact in a unimanual continuous coordination task.

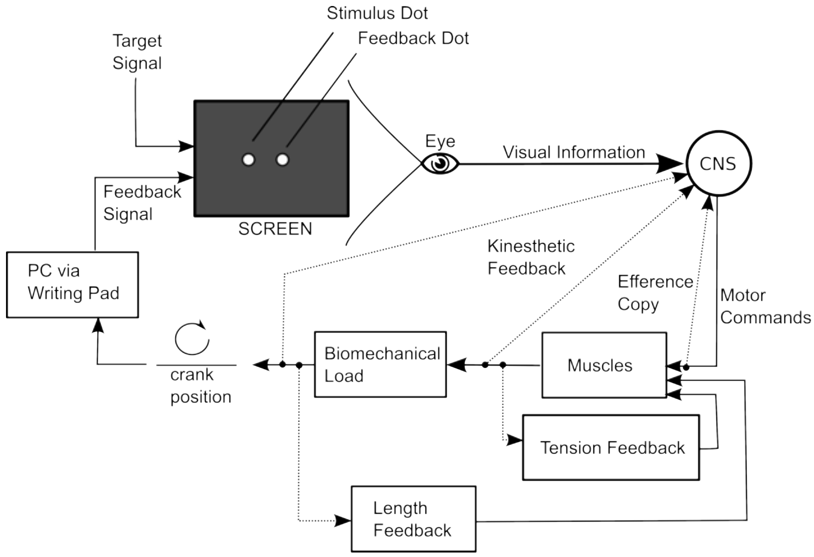

Figure 1.1: Model of action-perception-cycle adapted from Neilson et al. (1995)

A simplified model of the perception-action cycle as we will study it is depicted in Figure 1.1 and will be explained in the following paragraph. It is adapted from Neilson, Neilson, and O'Dwyer (1995), who used it to illustrate visual tracking tasks[1]. The experimental setting can be divided into an external part (environment) and an internal part (body). Participants monitored an external event, i.e. the circling of the stimulus dot on the screen. Their task was to coordinate their own hand movement with this stimulus by keeping the visual effect of their hand movement aligned with the stimulus. The internal part of the task required visual information about the position of the stimulus and feedback dot to be transfered to the CNS via the retina. Considering this information, the CNS generated motor commands which activate muscles. Muscles contracted and moved bones and thereby canged the angles of the involved joints. The resulting hand movements rotated

[1]We use a somewhat simplified version of the diagram by (Neilson et al., 1995, p. 101, Figure 1), the major changes are that the authors employed a *joystick* which we replaced by *crank position* and that we specified their *tracking system* with the means we used to collect and process movement date, i.e. writing pad connected to a PC.

the crank. Feedback about muscles and their biomechanical load (muscle tension, muscle length and joint angles) went back to the CNS. The external part, which consisted of the experimental apparatus that recoded and processed the crank position and presented the resulting feedback on the screen, was open to a range of experimental manipulations. We manipulated the congruency between the actual hand movement and its visual feedback as well as features of the visual display itself. The dissociation of the hand movement from its visual feedback should enable us to answer the question whether coordination with an external event takes place between the hand movement and the event or rather between the event and the visual effect of the hand movement. The influence of visual information about event and the visual movement effect for the accurate execution of the movement might be illustrated by systematically manipulating the visual setup of the paradigm. It has been shown that visual constraints can affect motor planning in the same way as physical constaints, especially in situations where distal effects have to be controlled (Palluel-Germain, Boy, Orliaguet, & Coello, 2004).

In coordination of movements with external stimuli, these stimuli add or reduce degrees of freedom to the system. It is important to understand which information may help coordination by reducing the degrees of freedom. Efferent and afferent motor signals and proprioceptive feedback can be used to control the position of the hand. Visual feedback about the environment can be used to control the external effects of movements. Part of the aim of this study is to try to find out which kind of feedback is preferred in order to control movements most efficiently.

1.2 Bimanual Coordination

The aim of studying perception-action relationships in bimanual coordination has brought forth different experimental strategies (Li, Levin, Carson, & Swinnen, 2004). There is the study of the relative phasing between two visual stimuli moving together, and between two movements performed simultaneously (Bingham, Schmidt, & Zaal, 1999; Zaal, Bingham, & Schmidt, 2000). There are paradigms that seperate bimanual coordination patterns from their visual perceptual consequences (Bogaerts, Buekers, Zaal, & Swinnen, 2003; Weigelt & Oliveira, 2003). Finally, there are studies where feedback is manipulated in a way to strengthen the visualization of the quality of interlimb coordination patterns (Byblow, Chua, & Goodman, 1995;

Mechsner, Kerzel, Knoblich, & Prinz, 2001; Swinnen, Lee, Verschueren, Serrien, & Bogearts, 1997).

In studies concerning the coordination of concurrent movements of the two hands, it became clear that as soon as the hands try to perform independent tasks, strong coupling effects occur. The fundamentals for the study of bimanual coordination were laid down in the seventies when motor coordination was mainly studied in order to determine whether it was under closed-loop feedback or open-loop programmed control (Adams, 1971, 1977; Schmidt, 1975).

In an experiment implying Fitts' Law (Fitts, 1954), Kelso, Southard, and Goodman (1979) demonstrated coupling effects between the two limbs. Fitts' Law basically gives a mathematical equation for speed-accuracy trade offs found in reaching tasks: the longer the amplitude and smaller the target, the slower the movement. Kelso et al. (1979) wondered what would happen if the two limbs perform two movements concurrently, for which Fitts' Law would make different predictions. Would the movement times still fit with the equation? As it turned out, they did not. Instead, the movement times were determined by the more difficult task[2] if the two hands had different instructions. The velocity and acceleration patterns of the two hands were very closely synchronized. Kelso interpreted this coupling as a means of the motor control system to reduce degrees of freedom when having to coordinate two movements with different characteristics.

In a later seminal paper Kelso (1984) pursued the matter of bimanual coordination further, this time introducing a paradigm that involved rhythmical movements of the fingers and hands. His observation was that when he asked participants to perform one movement cycle at every beat of a metronome and then increased its pace, spontaneous switches into the so called in-phase pattern occurred. This movement pattern involves the simultaneous contraction of homologous muscles and a phase difference of 0°. At slow speeds participants could also perform a second stable pattern, the so called anti-phase pattern, which involves muscle contraction in alternating fashion and, results in a phase difference of 180°. However, after frequency reaches a critical value, only the in-phase pattern remains stable. Participants switch from anti-phase to in-phase patterns and maintain this pattern even if

[2]Participants had to move their index finger from a home key to a target. Difficulty of the task was manipulated by the distance to the traget (6cm or 24cm) and the width of the target (7.2cm vs 3.6cm

frequency is reduced again. These results have been mathematically laid down in the Haken-Kelso-Bunz model (Haken, Kelso, & Bunz, 1985).
Another descriptive example for the coupling of the hands is offered by Franz, Zelaznik, and McCabe (1991), who asked participants to draw a circle with one hand and a vertical line with the other. The resulting shapes for both hands were vertical ellipses. Thus, the spatial parameters of the movements of the two hands seem to be mutually dependend. The spatial constraints governing motor coordination can be subdivided into the *egocentric* constraint and the *allocentric* constraint (Swinnen, Jardin, Meulenbroek, Dounskaia, & Hofkens-Van Den Brandt, 1997). The egocentric constraint describes movements that are made in mirror symmetry, which usually involves employing similar muscles in the limbs at the same time. The allocentric constraint applies to movements made in the same direction in external space, e.g. to the left or the right. For bimanual movements, the egocentric constraint usually dominates the allocentric constraint (Swinnen, Jardin, et al., 1997). For rhythmic bimanual movement patterns there is a strong tendency to perform mirror symmetric movements. Participants instructed to perform movements with 180° phase difference in a finger oscillation task for example, tend to switch to movements with 0° phase difference, especially if motor demands are increased (e.g. by requesting higher movement velocity). Reasons for these effects were seen in motor coupling processes involving the use of homologous muscles.

The limbs are obviously attracted by patterns that involve a high degree of synchrony. Kelso's (1984) results have been replicated in a number of studies using different paradigms 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). These results led to the conclusion that the preference for symmetric patterns is due to the symmetrical organization of the neuromuscular skeletal system. When trying to discuss the question of where this symmetry bias comes from, one should take a closer look at symmetry itself. In the aforementioned studies, three kinds of symmetry overlap (see also Tomatsu & Ohtsuki, 2005): (1) anatomical symmetry which means that homologous muscles in the two limbs are contracted simultaneously, (2) spatial symmetry, these muscle activations lead to mirrored movements in space, (e.g. both hand move towards the body midline), (3) visual symmetry, the visually perceived effects of the movements appear as mirror images of each other. A study by Mechsner et al. (2001) broke up this trinity of symmetry. They asked participants to perform finger oscillation movements in mirror symmetry or in parallel. By placing the hands one palm down, one palm up, they created incongruent conditions where anatomical symmetry no longer went along with spatial and visual symmetry (see Figure 1.2). The results show that in incongruent conditions participants benefited from spatial/visual symmetry but not from anatomical symmetry. The authors concluded, that bimanual movements are controlled by representations of their perceptual goals and the motor activations needed are "spontaneously and flexibly tuned in" (Mechsner et al., 2001, p.69).

Mechsner et al.'s (2001) results and their interpretation represent what might be called the *perceptual view* on motor coordination. It is assumed that the visual relationship between two moving objects is important for the stability of their coordination (Mechsner et al., 2001; Zaal et al., 2000). The opposing and more traditional *motoric view* argues that bimanual coordination benefits from homologue muscle activation in the two limbs and this simultaneous activation is the reason why in-phase coordination is that stable (Kelso, 1984; Byblow, Summers, Semjen, Wuyts, & Carson, 1999; Swinnen, Lee, et al., 1997).

1.3 Dissociations Between Action and Effect

One way to look closer at the contribution of motor constraints compared to visual perceptual limitations that are involved in motor coordination is to separate movements from their visual effects by means of transformed feedback. This approach has been used in unimanual (Roerdink, Peper, & Beek, 2005) as well as in bimanual tasks (Tomatsu & Ohtsuki, 2005; Mechsner et al., 2001; Bogaerts et al., 2003). Most of these studies show same results i.e. when a rather complicated motor task results in simple homogeneous visual feedback, performance in that task improves.

For example, when asked to perform bimanual circling with a 4:3 frequency ratio, participants fail and still have difficulties after extensive practise. However, participants can perform such an impossible task if it results in visual mirror symmetric effects. In the study by Mechsner et al. (2001) participants circled cranks with their hands invisible while a gear system translated the 4:3 ratio of the hands into mirror symmetric movement patterns of two visible flags (see Figure 1.3). Now participants could produce the instructed ratio. The importance of perception-action

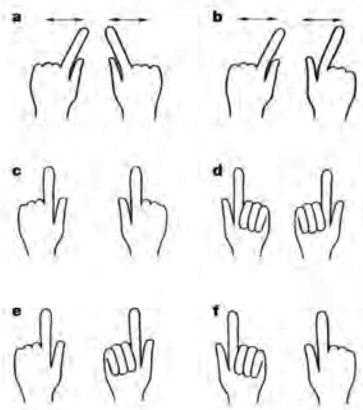

Figure 1.2: Experimental setup of Mechsner et al.'s (2001) study. a) symmetric movement, b) parallel movement, c) & d) congruent hand positions with both palms up or down results in visual symmetry AND anatomical symmetry, e) & f) incongruent hand positions with one palm up, one palm down results in visual symmetry OR anatomical symmetry

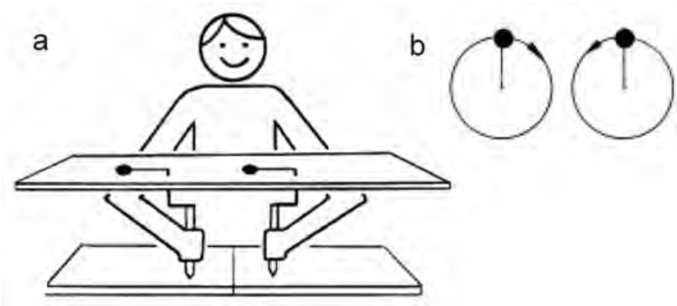

Figure 1.3: a) Experimental setup of Experiment 3 Mechsner et al. (2001). Participants circled cranks under the table in a 3:4 ratio while the flags on the table showed mirror symmetric movement (b)

coupling in bimanual coordination and the potential benefit of transformations in the production of complex movements was investigated by Bogaerts et al. (2003). They asked participants to perform orthogonal hand movements both in-phase and anti-phase and presented either regular (orthogonal) or transformed (parallel) visual effects (see Figure 1.4). Participants showed lower error rates for transformed feedback conditions for the perpendicular patterns. That is, they benefited from transformed feedback that resulted in coherently grouped, (i.e. parallel), motion structures. Similar effects could also be shown in an unimanual paradigm. In a visual tracking task employing in-phase and anti-phase tracking, Roerdink et al. (2005) showed that mirrored feedback improved anti-phase tracking as it resulted in visual in-phase movement patterns.

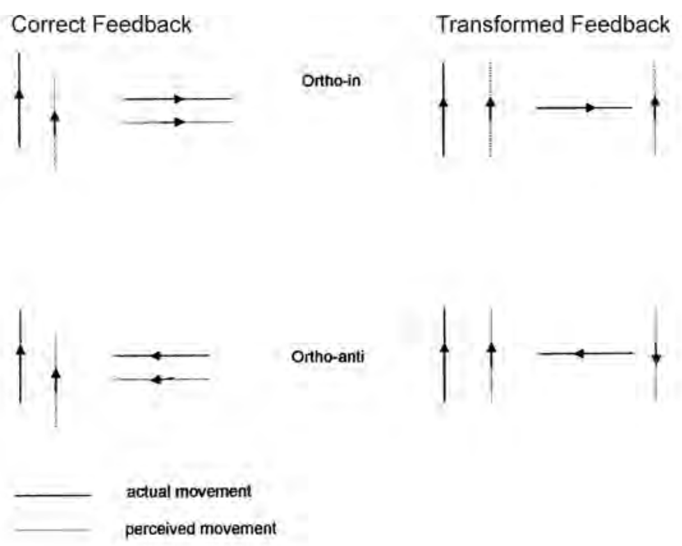

Figure 1.4: Experimental setup of the Bogaerts et al. (2003) study. Coordination of orthogonal movements proved to be easier with transformed feedback than with correct feedback.

Alaerts, Levin, and Swinnen (2007) went one step further and tried to distinguish between the impact of kinesthetic and visual feedback in a unimanual tracking task (see Figure 1.5). For the visual tracking participants saw a dummy arm and had to track its movement with their own left arm. For the kinesthetic tracking, the participants' right arm was moved passively while they were blindfolded and they had to track this with the left arm again. In the visuo-kinesthetic tracking task, participants could see the passive movement of their right arm and again had to track it with their left. Participants were instructed to produce mirror symmetric or parallel tracking. First of all, the results show that tracking performance was best when participants had both visual and kinesthetic feedback. For the question of whether participants benefited more from visual or kinesthetic feedback, they found a dependency on the instructed tracking mode. Parallel tracking was better with visual feedback while mirror symmetric tracking was superior with kinesthetic tracking. The authors interpret these results as showing that when only proprioceptive feedback is available, it is more beneficial to encode the movement in an egocentric reference frame (i.e. move towards and away from the body midline simultaneously) However, if only visual information is available, encoding in an allocentric reference frame is more beneficial. Those findings emphasize the point previously made, that the CNS flexibly adapts its strategies to the requirements of the current situation. However, if available, visual feedback seems to be valued rather highly as a source of information in both the state of the system and the environment.

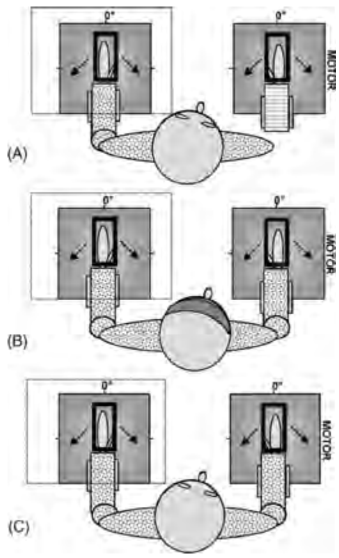

Figure 1.5: A) visual tracking, B) kinesthetic tracking, C) visuo-kinesthetic tracking, adopted from Alaerts et al. 2007

With continuous movements, which are, in contrast to discrete movements, subject to online corrections, visual feedback seems to play an especially important role in the adjustment of these movements to external requirements. Visual direction information can even overrule tactile direction information. In a study by Craig (2006) participants had to judge whether a tactile stimulation moved towards or away from them while they watched a visual stimulus moving towards or away from them. They were told to ignore the visual stimulus and only to judge the direction of the tactile stimulus. The results show that participants were unable to do so. When visual motion and tactile motion were presented at the same time but in different directions participants could only judge 42% of these incongruent trials correctly (compared to 93% in the congruent trials). The effect even remained present when the physical distance between the tactile and visual display was increased (near condition: visual display directly over the tactile display; far condition: visual display 28.5 cm in front of tactile display) or when tactile and visual display were rotated by 45 degrees. Most importantly, participants were highly confident in their wrong judgements, i.e. their poor performance was not due to insecurity because of interference. Rather, the tactile motion was captured by the visual motion.

The two studies just described show that vision seems to be rated as rather superior by the CNS compared to kinesthetic and tactile feedback. Normal participants seem to be quite limited in their awareness and monitoring of the actual bodily movements they perform if devoid of visual feedback. Fourneret and Jeannerod (1998) demonstrated this in a study where participants were asked to draw straight lines towards a target while the visual effect of their unseen hand movements was perturbed. Participants corrected their movements in order to produce a straight line but ignored the proprioceptive feedback telling them that the direction of the hand movement was not straight ahead. Similar results were found by Koblich and Kircher (2004) who used a circle drawing task and manipulated the visuomotor coupling by changing relative velocity of the visual effect. Participants compensated for changes without consciously detecting them until there were considerable discrepancies. Beers, Wolpert, and Haggart (2002) found that the weighting of vision compared to proprioception depends on the direction that has to be judged. Participants showed a preference for visual information if a target had to be located either left or right of the body midline. If the target had to be located near or far from the body (i.e. depth had to be processed) proprioceptive information was more beneficial. The authors argue that the brain weights information for the different modalities in order to reduce noise and chooses the source of information that minimizes uncertainty. The authors also propose that the reliance on proprioceptive information is much higher in everyday life and they point out that the weighting of information is flexible and it might therefore be misleading to say that one dominates the other.

Thus, the fact that proprioceptive feedback seems to be subordinate to visual feedback in some tasks and not consciously accessible in many situations does not mean that it is not important for movement coordination. Comparisons of control subjects with deafferented subjects show that the latter were less accurate and more variable in their movements and their spatial error was twice as large as that of the control subjects (Guedon, Gauthier, Cole, Vercher, & Blouin, 1998). The authors conclude that proprioceptive feedback is used to modify the calibration of the visuomanual tracking system when there are alterations in the visuomanual relationship.

Visual feedback allows us to monitor the effects of our actions in our environment. It is therefore reasonable that this kind of feedback is rated rather highly compared to proprioceptive feedback for example, which only tells us what our limbs are doing at the time. We act to achieve changes in our environment, which can best be monitored through vision. The effects or goals of our actions are what is important. This was demonstrated in a study with preschoolers and adults (Wohlschläger, Gattis, & Bekkering, 2003). The children were asked to imitate an adult model who reached for his ear. This could either happen in ipsilateral fashion i.e. right hand to right ear and left hand to left ear, or in contralateral fashion i.e. right hand reaching for left ear and left hand reaching for right ear. The children were mostly correct for the ipsilateral movements but for the contralateral, they had an error rate of up to 50%, reaching for the correct ear but with the *wrong* ipsilateral hand. They did not imitate the crossing movement. With adults, these mistakes did not happen but the same effect was found in the reaction times.

These results are in accordance with the ideomotor principle, which states that actions are represented by their intended effect. Sensory events are closely connected to the movements that brought them forth and the anticipation of such a sensory event is sufficient to activate the according movement. The ideomotor principle goes back as far as William James who states that: "Every representation of a movement awakens to some degree the actual movement which is its object." (James, 1890, Vol. II p. 526). A typical example of ideomotor movements taken from Lotze (1852) is that of bowling. If one observes someone who bowls a ball and then follows its course, one might recognize hand or body movements that seem to try to nudge the ball, although those movements clearly have no impact on the trajectory of the ball. The interpretation of these movements could be either that the seen movement of the ball is copied by the the body movements, this is called perceptual induction; (Knuf, Aschersleben, & Prinz, 2001)), or that the movements performed are those wished to be seen; this is called intentional induction. In a study using a billiard like paradigm strong evidence for intentional induction in hand movements was found (Knuf et al., 2001). This means that, at least for instrumented effectors, our intentions concerning an object are enough to involuntarily produce a movement that might be suited to fullfill those intentions, especially in situations when the connection between the movement and its effect is well learned.

1.4 Rationale of the Present Study

In action-to-event coordination, e.g. when we coordinate movements of our hands with events in extracorporeal space, the question arises what is actually coordinated with the external event. It could be that the actual hand movement is coordinated (movement-to-stimulus coordination); this would mean that the features of this movements in relation to the event are important for coordination. Ideomotor theory, however, would imply that the important relation is the one between the effect of the hand movement and the external event (effect-to-stimulus coordination). There are some results of previous studies which can be interpreted to support effect-to-stimulus coordination, like those of Mechsner et al. (2001) (3:4 circling task) or results that show that anti-phase unimanual tracking improves with mirrored feedback (Roerdink et al., 2005). Still there is the need for research that focuses on unimanual coordination with the explicit aim of comparing movement-to-stimulus coordination with effect-to-stimulus coordination. In addition, there is the need for a paradigm that allows the investigation of action-to-event coordination more closely in order to identify beneficial or disruptive stimulus-movement or stimulus-effect relations.

We adapted a classical bimanual paradigm to study unimanual coordination of continuous hand movements with external events. The paradigm used allows a wide range of systematic manipulations of A) the visual setup in which the movement effects were presented, B) the relation between movement and effect by means of different transformations and C) gradual manipulation of transformation magnitude. With this, we tried to distinguish the mechanisms of action to event coordination (i.e. the importance of visual feedback compared to the actual movement for coordination) and the impact of transformations on the accuracy of coordination. To investigate the coordination of unimanual movements with external events, we used a circling task that required participants to coordinate their hand movements with a clockwise circling stimulus. Trajectories of stimulus and effect were either presented next to each other (Experiment 1), within each other (Experiment 2) or on top of each other (Experiment 3). We varied movement rotation (symmetry/parallel) and movement phase (in-phase/anti-phase). To dissociate movements from their effects, participants performed the tasks under regular and transformed feedback.

We chose a continuous task as it would be closed-loop controlled i.e. open to visual and proprioceptive feedback and online corrections. There is evidence from patient studies implying that seperate neural systems exist for the control of discontinuos vs continous movements (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). The authors argue that discontinous movements are characterized by salient events which are controlled by explicit temporal goals, whereas continous movement timing is emergent. This should make a difference in the effects we expect as shown a study by Obhi and Haggard (2004). Participants had to perform non-repetitive flexion or extension movements of their index fingers with a congruent vs incongruent motor or external spatial relationship. Based on results from continuous repetitive movements, one would expect a symmetry benefit in the external congruent/motor incongruent (no homologue muscles) compared to the external incongruent/motor congruent (homologue muscles) (e.g. Mechsner et al., 2001). However, this symmetry benefit was not found. The authors conclude that for continuous tasks, feedback may be represented in external space whereas preprogrammed discrete movements do not require this kind of feedback, and that the significance of external spatial factors cannot be generalized onto discrete tasks.
Our decision for a circling task rather than an oscillation paradigm is based on the fact that oscillation movements always include salient proprioceptive turning points. This might invite participants to synchronize only those points and not continuously monitor their movements. Another example would be the maximum flexion of the finger in tapping, which is used for temporal coupling. With circling movements, there are no such positions that offer particular salient feedback, so participants should constantly monitor their movements. Experimental evidence for that assumption comes from studies that compared temporal variability between tapping

and circle drawing, and found that these are not correlated (Robertson et al., 1999; Zelaznik, Spencer, & Ivry, 2002).

For distinct movements, the importance of distal action effects has been shown (Massen & Prinz, 2007; Rieger, Knoblich, & Prinz, 2005). We aim to investigate if these results can be transfered to unimanual continuous movements, and how the importance of distal effects is modulated by visual setup and the action-feedback relation.

One of the perceptual features that will be investigated is the role of symmetry in unimanual coordination. If visual symmetry is a superordinate construct helping coordination in general, a symmetry benefit should show in the unimanual task as well. This is likely if it is true that the symmetry benefit in bimanual tasks mainly stems from perceptual features (Mechsner et al., 2001; Mechsner, 2004). If symmetry does not prove to be as crucial in unimanual coordination as in bimanual coordination, it will be interesting to identify other common features of stimulus, movement and effect that affect the quality of coordination performance.

Mechsner et al. (2001) showed that even impossible movements can be accomplished with easy visual feedback. Does this mean that however different the movement is from its effect, if it results in homogeneous feedback, participants will be able to perform the task? Or is there a threshold of how far movement and effect can be separated before performance breaks down? These questions will be addressed by introducing different transformations between the hand movement and its visual effect and by manipulating the magnitude of those transformations.

Chapter 2

General Methods

The paradigm described was the standard procedure and was used for most of the experiments reported. Any variations in setup or method will be reported in the methods section of the respective experiment.

2.1 Participants

Healthy adults were paid seven Euros/hour to participate in a single session. All participants had normal or corrected to normal vision and all were right handed.

2.2 Apparatus and Stimuli

The experiment was programmed using the C-language working on Microsoft DOS. Movements were recorded using a Wacom UD A3 writing pad at a resolution of 500 pixels per cm and a rate of 100 Hz, which was connected via serial port and was positioned about the navel level of the participants. Stimuli were presented on a 17 inch screen with a resolution of 800x600 pixels and a refresh rate of 75 hz. The center of the screen was aligned with the mid-sagittal axis of the participant's body. The background of the screen was black. On its left side, the stimulus was presented as a white dot (diameter=10 pixels) moving clockwise on a circular trajectory (radius=100 pixels). On the right side of the screen was a second white dot that was controlled by a stylus for the writing pad which was fixed inside a crank (radius 5 cm) that participants held (radius of visual trajectory=100 pixels). This dot will henceforth be called feedback. The hand was shielded from view. The centers of the trajectories of the dots were aligned at the horizontal midline of the screen. The center of the trajectory of the stimulus was 200 pixels from the left edge of the screen, and the center of the trajectory of the feedback was 200 pixels from the right edge of the screen. The distance between the two centers was 400 pixels. The center of the trajectory of the hand was positioned 10 cm to the right of the middle of the screen; correspondingly, participants performed the movement to the right of the body midline. We chose this setting to make the movement more comfortable for the participants and to keep the congruence between the movement and the presented effect as high as possible. Participants sat at a height-adjustable chair at a distance of about 60 cm from the screen. They were asked to remain an upright sitting position but were not fixed in any way (see Figure 2.1).

Figure 2.1: Experimental setup for the experiments. Participants sat at a table in front of a computer screen, with their hand shielded from view. In their right hand, they held the stylus of a writing pad which was fixed in a crank.

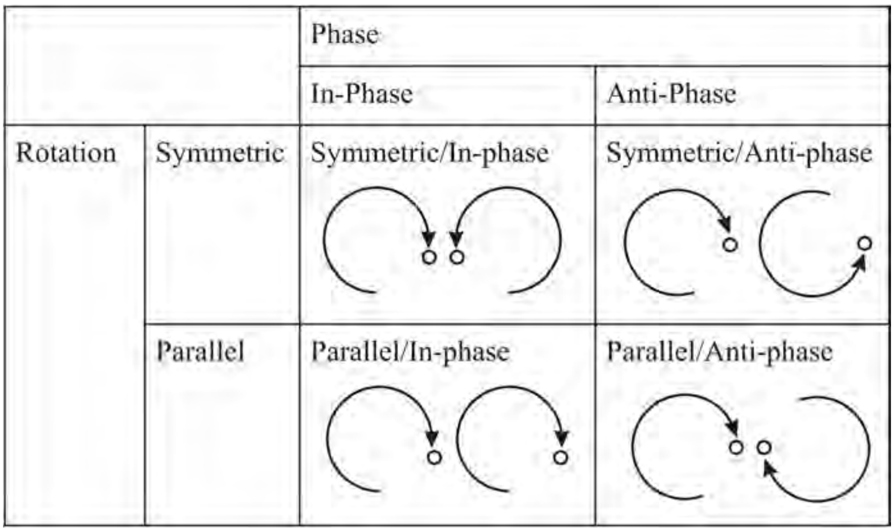

Figure 2.2: Illustration of the four patterns for the standard experiment. Circles symbolize positon of the stimulus dot or the effect dot, arrows symbolize movement direction.

2.3 Procedure and Design

Participants had to produce either symmetric or parallel patterns of the stimulus and the effect, which were either in-phase or 180° anti-phase (see Figure 2.2). Because the stimulus dot was always moving clockwise, participants had to move their hands in counter-clockwise direction to produce symmetry and clockwise in the parallel conditions (dots move in the same direction). For the symmetry/in-phase condition, the dots moved in perfect mirror symmetry, while for the parallel/in-phase condition, the effect dot copied the movement of the stimulus dot. For the anti-phase condition the effect dot always had to be 180° away from the in-phase position (see Figure 1). For half of the trials, the feedback was manipulated by a 180° phase shift between the position of the hand and the position of the visual feedback on the screen. This resulted in opposite coordination patterns between feedback and hand, i.e. visual in-phase goes along with movement anti-phase, and visual anti-phase goes along with movement in-phase.

Participants read printed instructions, in which the four different coordination modes were explained to these. Then they were shown a demonstration of them. Participants had the opportunity to ask questions in the instruction phase as well as later during the experiment prior to each trial, as an experimenter was present during the whole experiment. When the participants were sure they knew what the different instructions meant they were asked to assume an upright position holding the crank in their right hand and attend to the monitor in front of them. The experiment started with a short trial in which participants were simply asked to turn the crank, both checking whether the writing pad worked properly and allowing the participants to familiarize themselves with the apparatus. After that the procedure was the same for each trial. At first a two word instruction for the next trial appeared on the screen. This instruction defined the coordinative pattern of the movement effect relative to the stimulus. The first word specified the direction of the circling movement (symmetric or parallel). The second word of the instruction concerned the spatial relation of the stimulus and the effect dot (in-phase or anti-phase). When the participants had read the instructions and were sure about what they had to do, they pressed the space key with their left hand and the trial started. The stimulus dot started circling at the rightmost position of the trajectory (East). Participants were instructed hold their hand at this position as well, i.e. in the regular trial, the feedback dot started at position east in the transformed feedback trial it started at position west. Every ten circles the stimulus increased its speed by 0.2 Hz, starting at 0.6 Hz and speeding up to 2.2 Hz. Thus, there were nine speed levels. Every trial lasted 80 seconds. After the end of the trial, the instruction for the next trial appeared. The feedback condition (regular or transformed) was blocked and the order of the blocks was counterbalanced between participants. Each block consisted of 24 trials. For each condition (symmetry/in-phase, symmetry/anti-phase, parallel/in-phase, parallel/anti-phase), two clusters consisting of three trials were presented. The order of the clusters was randomized within the transformation and no-transformation blocks. Altogether the participants had to complete 48 trials. Effective testing time was 64 minutes. However the time it took participants to complete a session varied between 1 hour 15 minutes and two hours and 15 minutes, because they had the opportunity to take breaks for as long as they wished to between the trials.

2.4 Data Analysis

In a first step, the position data were interpolated to yield a constant sample rate of 100 Hz because there was some variation in the sampling period of the writing pad (7 to 13 ms). The first trial of each condition was considered a training trial and excluded from analysis. We also excluded the first three stimulus circles of every speed level to give the participants time to adapt to the new requirements. The following dependent variables were calculated: To assess the quality of interlimb coordination, we calculated the Constant Error (CE), a signed value calculated by subtracting the ideal angle of the effect from the actual angle. Because the shortest distance between the two points was used, the CE cannot be higher then 180 degrees. The CE indicates whether participants are ahead (positive values) or behind (negative values) their supposed position. Note that this value can only be interpreted in a straightforward manner if participants essentially perform the pattern as instructed. To further analyze how well participants performed the instructed pattern and whether they fell into a movement mode contrary to the instructed mode, we calculated the percentage of time participants spent in the Instructed Mode (IM) and in the Contrary Mode (CM). IM was defined as absolute value of CE between 0° and 45° and CM was defined as absolute value of CE between 135° and 180°. Thus, the expected value (if performance is random) is 25% for these dependent variables. Note that even though we interpret IM and CM as measures of spatial accuracy, they also have temporal implications. In order to produce the instructed pattern, participants have to adjust their movement speed to the speed of the stimulus, which can be also interpreted as a visual pace maker.

Trajectories of continuous movements are often scratchy and asymmetrical rather than perfectly smooth and symmetric. Nevertheless, they are characterized as regions of reduced kinematic variability, often located around maximal angular excursions or movement endpoints (Roerdink et al., 2005; Roerdink, Ophoff, Peper, & Beek, 2008; Byblow et al., 1994). These regions have been called "anchor points" and it is suggested that they serve as "attentional attractors" or "organizing centers" for the movement production (Beek, 1989). The use of anchoring in our paradigm and especially differences in regions used for anchoring between the visual setup manipulations could bring useful insight into how visual information is inconcorporated into motor coordination.

To investigate the use of anchoring, we calculated the variable error (VE) at 24 sections of 15° covering the full 360° of the stimulus trajectory. The VE is the standard deviation around the CE. To calculate this measure, all CE values corresponding to values of the stimulus dot within the respective section were averaged

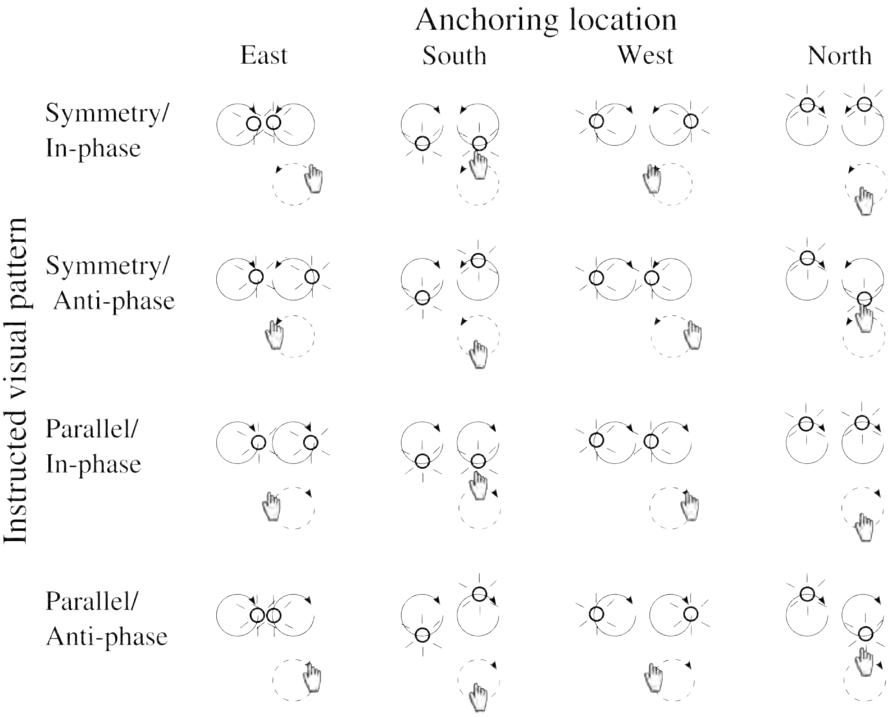

Figure 2.3: The illustration shows the tested anchoring locations and the corresponding hand positions for conditions with feedback shifted by 180°. Note that for regular feedback conditions, the hand positions match the position of the visual feedback.

for each circle. Then the standard deviation across circles was calculated from those values. The CE describes the variability of the movement position across consecutive circles at those sections. For the interpretation of the data, we will use North, East, South and West (as in a compass) as salient locations on the trajectory (see 2.3). Additionally, sometimes values in degrees out of 360 will be given with East matching 0° and a clockwise increase, i.e. south = 90°, west = 180° and north = 270°. We will only report effects that add to our knowledge from the analysis of IM and CE in order to focus on answering the above questions.

Because performance deteriorated with faster speeds and no clear coordinative patterns emerged, we only included the five slower speed levels in the following analysis. Unless otherwise stated, repeated measures ANOVAs were conducted with the factors Feedback (regular, transformed), Direction (symmetric, parallel), Phase (in-phase, anti-phase) and Speed (0.6 Hz, 0.8 Hz, 1 Hz, 1.2 Hz, 1.4 Hz) on the dependent variables. Only significant effects are reported. Paired sample t-tests ($p < 0.05$) were used for post-hoc analysis.

Chapter 3

Part I - Influence of Visual Display

3.1 Introduction

Many everyday activities require people to coordinate their actions with events in the environment. Directing one's way through a moving crowd, or dribbling a basketball are examples of such activities. We rely on this coordinative ability so much that failure has severe consequences. If, for instance, in a crowded street, we fail to adjust our movements to the speed and the direction of the people approaching from the side, we may bump into them and this may cause unwanted interpersonal contact and physical pain. Even though coordination with events in the environment is very important for our everyday lives, it is still controversial how this ability works. Most of the research on coordination principles has been done in the area of bimanual coordination, i.e. coordination of the two hands with each other. Most of the research in unimanual coordination, i.e. coordination of the movement of one hand with a stimulus, has been conducted with respect to rhythmic movements as in tapping (e.g. Aschersleben & Prinz, 1995) or using coincidence anticipation tasks (e.g. Fleury, Bard, Gagnon, & Teasdale, 1992). Much less is known about visuo-spatial coordination of continuous movements, which we investigated in the present study. We will now first review research on bimanual coordination, because the coordination principles identified in bimanual research are also used to discuss results in unimanual coordination studies (e.g. Alaerts et al., 2007). After that, we will turn to research on unimanual coordination in the visuo-spatial domain.

Research on bimanual coordination demonstrated that people are better at performing some movement patterns than others. Generally, people are more accurate and consistent in their performance if they execute bilateral mirror symmetric movements than when they perform any other type of movement pattern. Mirror-symmetric movements are movements in which the homologous limbs move towards and away from the body midline at the same time (e.g. one hand is rotated clockwise and the other hand is rotated counter-clockwise). Those movements inherit homologous muscle activations as well as homologous proprioception of the movements of the limbs. The finding that these are quite stable and accurately performed is sometimes referred to as the egocentric constraint (Swinnen, Jardin, et al., 1997), describing a constraint located within the body, which could either be based on the movement itself or on the proprioception of the limbs. Further, it is also advantageous to move two limbs into the same direction in external space, that is, in parallel (e.g. moving both hands to the left). This is sometimes referred to as the allocentric constraint (Swinnen, Jardin, et al., 1997), describing a constraint located in external space. Further, movement performance is more stable when the coordination mode is in-phase (the two hands are at the same position on their trajectory) than when they are anti-phase (the positions of the hands on the trajectories are shifted by 180°). Intermediate modes are even less stable (Haken et al., 1985; Tomatsu & Ohtsuki, 2005). Increased movement speed not only increases differences in performance stability but can also evoke switches from less stable anti-phase mode into stable in-phase mode (Carson et al., 1997; Haken et al., 1985; Kelso, 1984; Wimmers, Beek, & Wieringen, 1992).

This general pattern of performance stability has led to several versions of so-called motor theories of bimanual coordination. In motor theories of bimanual coordination, it is assumed that the coactivation of homologous muscles (Kelso, 1984), or a more efficient movement parameter specification by the brain (Oliveira, 2002; Heuer, 1993) plays a major role in the observed symmetry benefit. In contrast, advocates of perceptual theories of bimanual coordination assume that performance advantages for symmetrical movements are not due to muscular activations, but rather due to the perceived symmetry (e.g. Mechsner et al., 2001). However, in a standard bimanual coordination task, it is not possible to distinguish between perceptual symmetry and motor symmetry. In order to dissociate perceptual and motor symmetry, investigators have used manipulated visual feedback by introducing a transformation between the movement and its visual feedback, for example by shifting the visual feedback of a circling movement (Mechsner, 2004; Tomatsu & Ohtsuki, 2005).

Several studies indicate that perceptual symmetry indeed plays an important role in bimanual coordination (e.g.Bogaerts et al., 2003; Mechsner et al., 2001; Mechsner, 2004). It has been shown that people prefer symmetric movements independent of the activation of homologous muscles in finger wriggling, tapping and circling tasks (Mechsner et al., 2001) and that visual feedback can alter performance in bimanual coordination tasks (Bogaerts et al., 2003).

However, not all studies dissociating movements from their effects find that visual space is more important than motor space for coordination (Salter, Wishart, Lee, & Simon, 2004). Still these results do not rule out a perceptual interpretation of movement coordination, as these movements might be coordinated with respect to proprioceptive effects. In accordance with this view, Mechsner et al. (2001) found a benefit for symmetric movements in a bimanual finger tapping task when participants had to rely on proprioception because they were not able to see their movements, even when the movements were produced using non-homologous fingers. This provides evidence that proprioceptive effects play an important role in bimanual coordination.

In unimanual coordination, there is no second limb with which movements need to be coordinated, but rather a coordinative stimulus. Since there can be no constraints on the motor level because the homologous limb is not moving, it is likely that unimanual coordination has to follow the perceptual characteristics of the movement and its effects, i.e. visual effects or the proprioception while performing the movement. Thus, unimanual coordination may take place between the movement itself and external stimuli (movement-to-stimulus-coordination) or visual effects of the movement and the external stimuli (effect-to-stimulus-coordination). Studies indicate effect-to-stimulus-coordination plays an important role in unimanual coordination (e.g.Buekers, Bogaerts, Swinnen, & Helsen, 2000; Roerdink et al., 2005).

In the present study, we used a continuous circling paradigm similar to the ones often used in bimanual research to examine interlimb coordination (e.g. Swinnen, Jardin, et al., 1997; Tomatsu & Ohtsuki, 2005). As we are interested in unimanual coordination, we replaced the second hand with a computer controlled stimulus. Participants had to perform unimanual continuous circling movements which had to be coordinated with a continuously circling dot on a computer screen. The first goal of the present study was to investigate whether unimanual action-to-event coordination follows the principle of movement-to-stimulus-coordination or effect-to-stimulus-coordination. To differentiate between these two possibilities, we dissociated movements from their effects by means of a transformation between them. All conditions were also performed with untransformed visual effects. If unimanual coordination follows the principle of effect-to-stimulus-coordination, we expect to observe the same performance pattern in visual space in both feedback conditions. However, if unimanual coordination follows the principle of movement-to-stimulus-coordination, different performance patterns in visual space in both feedback conditions are expected. In addition, we wanted to investigate whether we would find evidence for anchoring as a means to coordinate own movements with an external stimulus. Anchoring is described as a reduction of variability of performance for salient positions in the movement trajectory and has been observed for bimanual (e.g. Byblow et al., 1994; Fink, Foo, Jirsa, & Kelso, 2000) and unimanual (Roerdink et al., 2008) tasks. Finally, we wanted to investigate whether we could influence task performance and coordination mechanisms by manipulating the layout of the visual setup. If the visual effects of movements are important for unimanual coordination, the way they are presented in relation to the stimulus in the environment should play an important role. We therefore varied the visual relationship between the circling stimulus dot and the effect dot in the three experiments we conducted.

In general, the visual context, i.e. the arrangement of movement effects in bimanual coordination and the arrangement of stimuli and movement effects in unimanual coordination, seems to play an important role in performance. In an unimanual coordination study Roerdink et al. (2005) had participants produce movements in the same or opposite direction of a stimulus under conditions of mirrored and normal feedback of their own movements. Participants' performance in producing movements in the direction opposite to the stimulus direction improved if they were provided with mirrored feedback, which meant that stimulus and movement effect moved in the same direction. Bogaerts et al. (2003) investigated coordination performance in a bimanual task. Participants had to move their hands either orthogonally or in parallel. Feedback was either orthogonal or parallel as well (i.e. the feedback for one hand was transformed in some conditions). When participants moved their hands orthogonally, error rates were smaller with parallel than with orthogonal feedback. Because the actual movement was the same in both conditions, any effects observed had to be due to the perceived visual feedback. Thus, feedback can aid performance, even if it is not congruent with the movement that produces it, if it results in coherently grouped visual motion structures. This may be due to Gestalt factors like common fate or proximity, which allow highly effective information processing (see Mechsner, 2003; Alaerts et al., 2007; Bogaerts et al., 2003).

3.2 Experiment 1

The task we used was adapted from bimanual circling tasks (see Swinnen, Jardin, et al., 1997; Tomatsu & Ohtsuki, 2005). Participants saw two circling dots on a screen that could very well be produced by two hands circling next to each other. However, as we were interested in unimanual coordination, only the right hand was circling, the left hand was “replaced” by a computer controlled stimulus. Participants had to produce symmetric and parallel patterns, which were either in-phase or 180° anti-phase. We only included patterns with clockwise movements of the stimulus and the respective movements of the right hands, because Swinnen, Jardin, et al. (1997) showed that there were no essential differences in the data patterns obtained from counter-clockwise and clockwise movements variations in the circling task, as long as the coordination pattern is the same.

Because perceived symmetry is beneficial in bimanual coordination (e.g. Mechsner et al., 2001), we expected to replicate the data pattern (Swinnen, Jardin, et al., 1997) obtained in their bimanual coordination task in the present unimanual coordination task. Thus, we expected better performance in symmetric than in parallel coordination patterns and better performance in in-phase than in anti-phase coordination patterns (Bogaerts et al., 2003; Mechsner et al., 2001; Swinnen, Jardin, et al., 1997). Further, we expected better performance in terms of accuracy and variability under conditions of visual in-phase than visual anti-phase. In order to investigate whether unimanual coordination follows the principle of movement-to-stimulus or effect-to-stimulus-coordination, all conditions were performed twice: once with regular feedback and once with transformed feedback (the effect position was presented 180° away from the movement position). We expected to obtain evidence of effect-to-stimulus-coordination. This implies that if we analyze performance with respect to the movement effects, the data pattern obtained should essentially be the same for the regular and the transformed condition. If differences in the observed data pattern of regular and transformed conditions exist, these differences must be due to movement-to-stimulus-coordination. With respect to anchoring, we expected that participants would show less variability in positions in which the effect dot is close to the stimulus dot, e.g. the east position (defined by the stimulus) in the symmetry/in-phase condition, than when they are further apart.

3.2.1 Method

For this experiment the standard setup was used (see Figure 3.1)[1].

Participants

Fourteen adults (three male and eleven female, aged 19 to 34 years) were paid seven Euros/hour to participate in a single session.

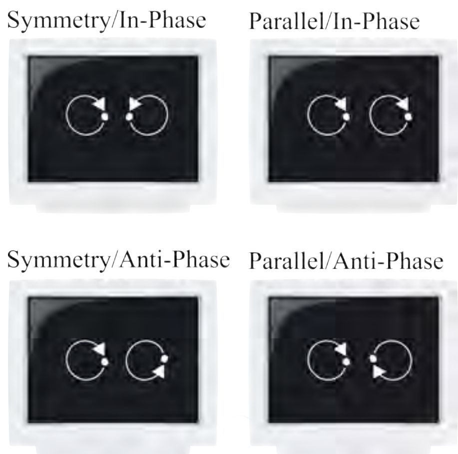

Figure 3.1: Illustration of the four patterns for Experiment 1. Circles symbolize position of stimulus dot or effect dot, arrows symbolize movement trajectory and direction.

[1]The instructions in German were: "Symmetrisch" for symmetry; "Parallel" for parallel; "Gleich" for in-phase; "Versetzt" for anti-phase.

3.2.2 Results

The results are graphically depicted in Figure 3.2. the means and standard deviations (averaged across speed levels) for the different dependent variables are given in Table 3.1.

	Regular feedback				Transformed feedback			
	Symmetric		Parallel		Symmetric		Parallel	
	In-Phase	Anti-Phase	In-Phase	Anti-Phase	In-Phase	Anti-Phase	In-Phase	Anti-Phase
	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)
Instructed Mode %	66 (16)	14 (8)	58 (17)	41 (13)	38 (11)	19 (5)	47 (18)	31 (7)
Contrary Mode %	4 (4)	36 (11)	6 (7)	11 (8)	13 (8)	31 (6)	12 (8)	18 (5)
Constant Error	20 (8)	*	26 (11)	16 (19)	22 (12)	*	-3 (13)	19 (11)
Variable Error - east	38 (16)	*	38 (20)	59 (17)	58 (13)	*	57 (15)	67 (9)
Variable Error - south	44 (17)	*	45 (22)	68 (22)	74 (19)	*	71 (21)	88 (14)
Variable Error - west	46 (18)	*	46 (24)	70 (20)	75 (20)	*	70 (21)	89 (12)
Variable Error - north	45 (18)	*	43 (22)	70 (22)	69 (18)	*	71 (21)	87 (13)

*Table 3.1: Note. All values for IM and CM differed significantly from the expected value for random performance (25%), * those values cannot be interpreted in a straightforward way because participants' performance was not predominantly in the instructed mode.*

Instructed Mode (IM) and Contrary to Instructed Mode (CM)

As can be seen in the upper part of Figure 3.2, under regular feedback conditions, participants tended to be most frequently in the IM in all but the symmetry/anti-phase condition. In the symmetry/anti-phase condition, participants seemed to be most frequently in the CM. In the transformed trials (lower part of Figure 2) there was a slight decrease in performance, but the data pattern is similar to the pattern with regular feedback.

An ANOVA on IM as a dependent variable confirmed those observations. There was a significant main effect of Speed, $F(4,52)=9.2$, $p=0.002$, indicating that the time spent in IM decreased with faster speeds. This effect was stronger with in-phase conditions compared to anti-phase conditions, resulting in a significant interaction of Speed x Phase, $F(4,52)=21.3$, $p<0.001$. This is probably due to a floor effect. In anti-phase trials, performance was already worse than in in-phase trials, therefore there was less scope for further decline. There was also a significant interaction of Speed x Rotation, $F(4,52)=3.9$, $p=0.008$, indicating a greater reduction in IM with increasing speed in parallel trials than in symmetric trials.

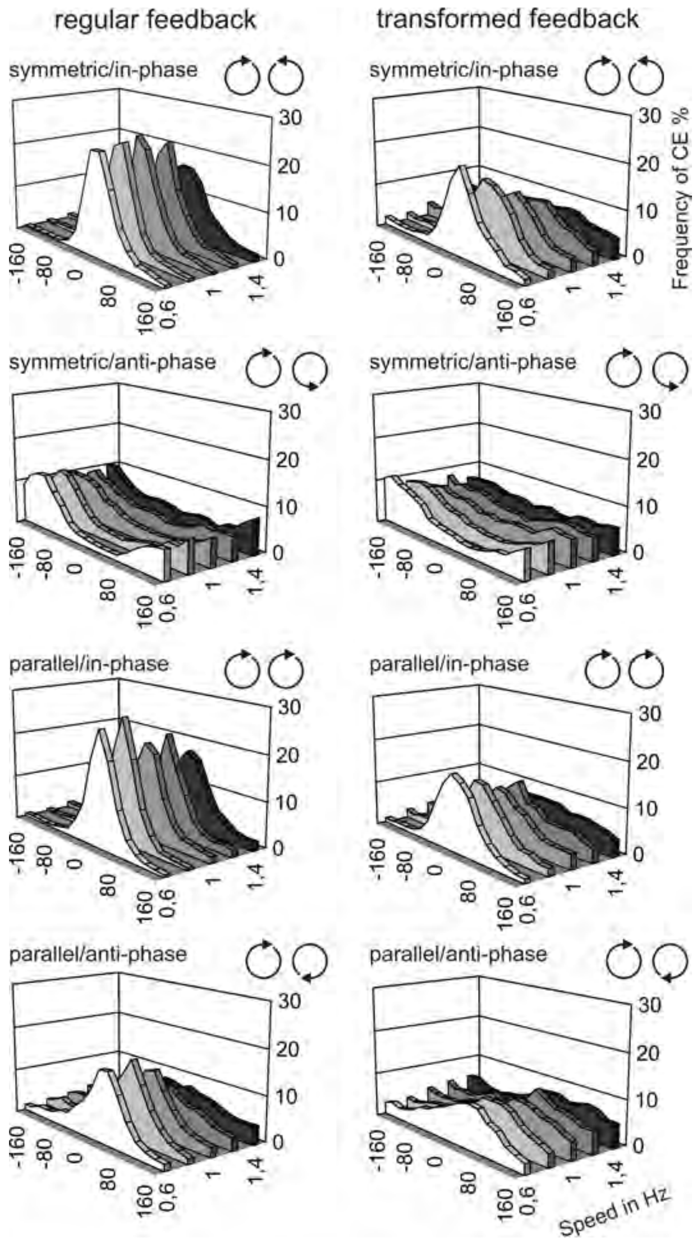

Figure 3.2: Frequency distributions (in %) for the Constant Error in Experiment 1 by speed level.

Further, there was a significant main effect of Feedback, $F(1,13)=31.6$, $p<0.001$, showing that under transformed feedback, IM was lower than under regular feedback. A significant interaction of Feedback x Speed, $F(4,52)=3.9$, $p=0.007$, shows that IM declined more in transformed trials than in regular trials with increasing speed. Most importantly however, none of the other interactions with feedback was significant, and none of the effects reversed with transformed feedback, indicating that feedback had no effects on the general performance pattern in visual space.

There was a significant main effect for Phase, $F(1,13)=53.8$, $p<0.001$, and a significant interaction of Rotation x Phase, $F(1,13)=23.9$, $p<0.001$. Participants always spent more time in IM in in-phase than in anti-phase conditions. Whereas IM did not differ between the two in-phase modes with respect to rotation, $t(13)=-0.4$, IM was lower in the symmetry/anti-phase patterns than in the parallel/anti-phase patterns, $t(13)=-5.4$, $p<0.001$.

To analyze CM, we performed one-sided t-tests to test whether participants were above chance in any of the conditions (condition data was combined over feedback). This was only the case for the symmetry/anti-phase condition, $t(13)=4.2$, $p=0.001$. CM was even higher than IM in this condition, $t(13)=-4.8$, $p<0.001$, indicating that participants produced predominantly a symmetric in-phase pattern in visual space, rather producing symmetry anti-phase, which was the instructed pattern.

Constant Error (CE)

The symmetry/anti-phase condition was not included in the analysis of CE, because IM was not better than chance in that condition. A repeated measures analysis with the factors Feedback (regular, transformed), Condition (symmetry/in-phase, parallel/in-phase, parallel/anti-phase) and Speed (0.6 Hz, 0.8 Hz, 1 Hz, 1.2 Hz, 1.4 Hz) was conducted on CE. As can been seen in Figure 2, CE was positive (participants preceded the stimulus) in all of the conditions analyzed. There was a main effect of speed, $F(4,52)=5$, $p=0.002$, showing that value of CE decreased with increasing speed. There was a significant decrease of CE for parallel/in-phase conditions, $t(13)=2.8$, $p=0.014$, with transformed feedback. However, feedback had no effect on symmetric/in-phase, $t(13)=0.5$, and parallel/anti-phase, $t(13)=0.6$, conditions, as a significant interaction of Feedback x Rotation, $F(2,26)=3.9$, $p=0.032$, shows.

Variable Error (VE)

A repeated measures ANOVA with the factors Condition (symmetry/in-phase, parallel/in-phase, parallel/anti-phase), Feedback (regular, transformed), Location (24 sections, each covering 15 degrees of the trajectory), and Speed (0.6 Hz, 0.8 Hz, 1 Hz, 1.2 Hz, 1.4 Hz) was conducted on VE. Again the symmetry/anti-phase condition was excluded because IM was not better than chance in that condition. We found the same pattern of results as in the error analysis, i.e. participants' variablity increased with speed, they were more variable with transformed feedback and were least variable in parallel/in-phase and symmetry/in-phase trials compared to parallel/anti-phase trials as is evident from main effects for Speed, $F(4,52)=30$, $p<0.001$, Feedback, $F(1,13)=73.3$, $p<0.001$ and Condition, $F(2,26)=21.6$, $p<0.001$. See Figure 3.3 for a depiction of the VE distribution.

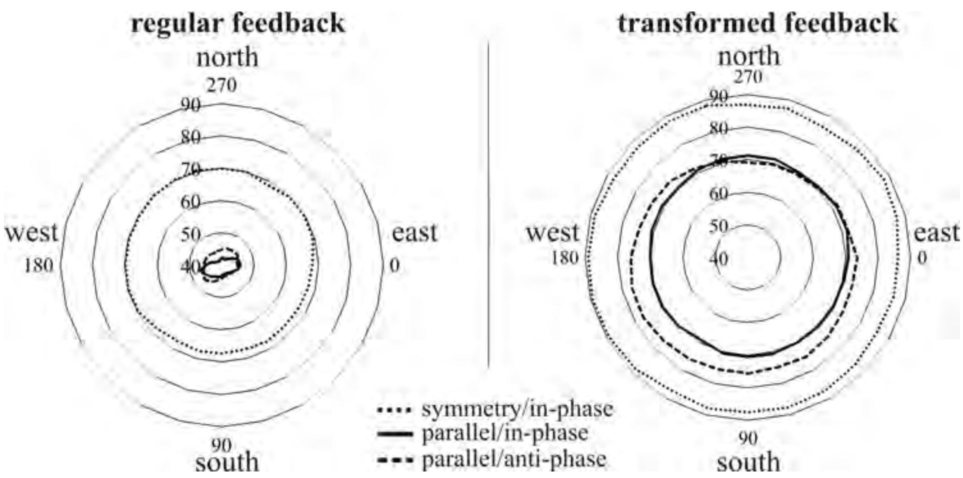

Figure 3.3: The distribution of the VE along the circular trajectory for the three conditions analyzed with regular and transformed feedback.

There was a main effect of location, $F(23, 299)=3,7$, $p<0.001$, showing that the participants performance was least variable in the north position and most variable in the west position, see Figure 3.2. This effect was strongest in the symmetric/in-phase condition as an interaction Location x Condition, $F(46,598)=2.7$, $p<0.001$, appeared. Overall however, location differences were minimal compared to condition differences.

3.2.3 Discussion

In the present experiment, participants performed unimanual continuous circling movements which varied in rotation (symmetry, parallel), and phase (in-phase, anti-phase) relative to a circling stimulus dot. Further, feedback of the movement was either regular or transformed by a 180° phase shift. Overall, the same performance pattern was obtained for regular and transformed feedback conditions. As expected, we found better performance in in-phase conditions than in anti-phase conditions, i.e. participants showed smaller deviations from their ideal position and stayed longer in the instructed movement pattern. Participants were not able to sustain the symmetry/anti-phase instructions, but instead fell into symmetry/in-phase (defined in terms of the visual pattern), regardless of whether the feedback was regular or transformed. Participants used location north for anchoring.

The observation that the overall performance pattern was similar for regular and transformed feedback conditions is consistent with the assumption that unimanual coordination follows the principle of effect-to-stimulus-coordination but not movement-to-stimulus-coordination. This is in accordance with previous studies (e.g. Bogaerts et al., 2003; Roerdink et al., 2005).

The overall pattern of results resembles the findings of Swinnen, Jardin, et al. (1997) on bimanual coordination. In this study in-phase performance exceeded anti-phase performance and symmetry/anti-phase conditions were most difficult for the participants. One interesting difference, however, is that in the present experiment no significant difference in performance between symmetry/in-phase and parallel/in-phase conditions was observed, whereas Swinnen, Jardin, et al. (1997) obtained better performance in the symmetry/in-phase condition than in the parallel/in-phase condition. They argue that the performance advantage of the symmetry/in-phase pattern is due to the egocentric constraint, that is, homologous muscles are activated in this condition. Because we used an unimanual task in the experiment, coactivation of homologous muscles cannot happen. It may well be that we obtained no difference between symmetric and parallel conditions because an egocentric constraint is not available and perceptually both symmetric and parallel conditions may be of equal difficulty.

Participants used the north position to synchronize their performance with the stimulus for all conditions. This implies that there is a benefit for this location inherent in the visual setup. More precisely, at this location, the movement direction in reference to the body changes from towards the body to away from the body and vice versa. If we interpret increased anchoring as a sign of higher coordination demands, the fact that anchoring is more pronounced for symmetry/in-phase conditions means that this condition is more difficult than parallel/in-phase, although this difference does not show itself in the error rates. In symmetry/in-phase conditions, the two dots move in different directions in extrinsic space and constantly change their distance to each other. It seems plausible that this pattern is harder to maintain then parallel/in-phase where the dots copy each other and keep a constant distance. This additional information about task demands validates anchoring analysis as a usefull tool to get a closer look at the coordination mechanisms involved.

3.3 Experiment 2

The results of Experiment 1 indicate that unimanual coordination is based on effect-to-stimulus-coordination and not on movement-to-stimulus-coordination. In the coordination of both symmetric and parallel movements, similar locations were used for anchoring the movements. To investigate these effects in further detail, we decided to manipulate the visual setup of the task in order to change the stimulus-effect relations in symmetric and parallel conditions in Experiment 2: Stimulus dot and effect dot were now presented on interleaved trajectories. Thus, the two dots circled around the same center. This made the trajectory of the stimulus as similar to the trajectory of the effect dot as possible. As a result, the trajectories in the symmetry/in-phase condition crossed at the locations north and south. If anchoring occurs at the points at which the trajectories are closest together, it should occur at those points in the symmetry/in-phase conditions. In the symmetry/anti-phase condition, the trajectories crossed at locations east and west. The movement pattern for the parallel condition is characterized by a constant distance between the effect dot and the stimulus dot. This arrangement is very close to tracking tasks, (e.g. Buekers et al., 2000) in which the spatial relations between stimulus and feedback are rather simple. Because of our manipulation, there are severe differences in the perceptual quality of the conditions. Therefore, we would expect no main effect of location for this experiment, in contrast to the effect found for location north in Experiment 1. Rather, the crossing points might be used for anchoring in the symmetric conditions.

For the parallel conditions, location north might still be used and indicate a general benefit of this location. We again expected that the general performance pattern would not differ between regular and transformed conditions and that performance in in-phase conditions would be better than in anti-phase conditions.

3.3.1 Method

Participants

Sixteen adults (three male and eleven female, aged 22 to 30 years) were paid seven Euros/hour to participate in a single sessions.

Apparatus and Stimuli

For this experiment, the trajectories of hand the same center which was in the also the center of the screen. The radius of the inner trajectory was 100 pixels, the radius of the outer trajectory was 120 pixels.

Procedure and design

For this experiment, the stimulus and feedback circled on interleaved trajectories. For an illustration of the effect pattern see Figure 3.4. Due to the visual setup, the distance between the two dots changed constantly in the symmetric conditions. In the symmetry/in-phase condition, the dots were always at the same distance from location south and crossed at the north and south location of the trajectories. In the symmetry/anti-phase condition, the two dots were always at the same distance from position west and crossed at the east and west locations of the trajectories. In the parallel/in-phase, condition the two dots were always next to each other, meaning that they ought to have the same angle in their trajectories all the time. In the parallel/anti-phase condition, the dots were supposed to always be on opposite positions of their trajectory. Thus, the distance of the dots was constant at either 180° for anti-phase or 0° for in-phase with parallel rotation[2].

[2]The instructions for the participants in German were: “Gleich” for parallel; “Entgegen” for symmetry; “A” for in-phase; “B” for anti-phase. We decided against using the instructions from experiment 1 as in the symmetric conditions mirror symmetry was not as obvious as in the previous experiment. This is why we defined the required movement direction in reference to the stimulus movement. As we could not use “Gleich” for both rotation and phase instruction, we decided on

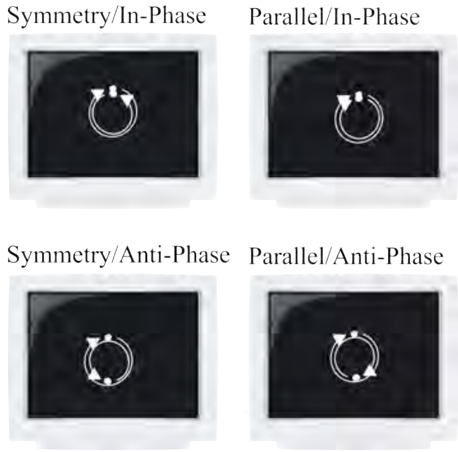

Figure 3.4: Illustration of the four patterns for Experiment 2. Circles symbolize position of stimulus dot or effect dot, arrows symbolize movement trajectory and direction.

3.3.2 Results

Figure 3.5 illustrates the performance in Experiment 2. The means and standard deviations (averaged across speed levels) for Experiment 2 are given in Table 3.2.

	Regular feedback				Transformed feedback			
	Symmetric		Parallel		Symmetric		Parallel	
	In-Phase	Anti-Phase	In-Phase	Anti-Phase	In-Phase	Anti-Phase	In-Phase	Anti-Phase
	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)
Instructed Mode %	50 (16)	15 (7)	88 (9)	53 (14)	42 (17)	18 (7)	68 (15)	41 (13)
Contrary Mode %	7 (7)	37 (11)	2 (3)	4 (5)	14 (8)	36 (12)	6 (5)	12 (7)
Constant Error	31 (12)	*	0 (1)	0 (1)	20 (9)	*	0 (1)	0 (1)
Variable Error - east	82 (12)	*	22 (11)	103 (16)	90 (12)	*	37 (12)	95 (15)
Variable Error - south	49 (17)	*	32 (15)	58 (9)	72 (18)	*	60 (20)	74 (12)
Variable Error - west	50 (19)	*	107 (12)	52 (8)	72 (19)	*	106 (13)	72 (13)
Variable Error - north	72 (26)	*	31 (14)	69 (19)	89 (21)	*	50 (17)	87 (15)

*Table 3.2: Note. All values for IM and CM differed significantly from the expected value for random performance (25%), * those values cannot be interpreted in a straightforward way because participants' performance was not predominantly in the instructed mode.*

symbolic letters. None of the participants had problems with the distinction of the different movement modes.

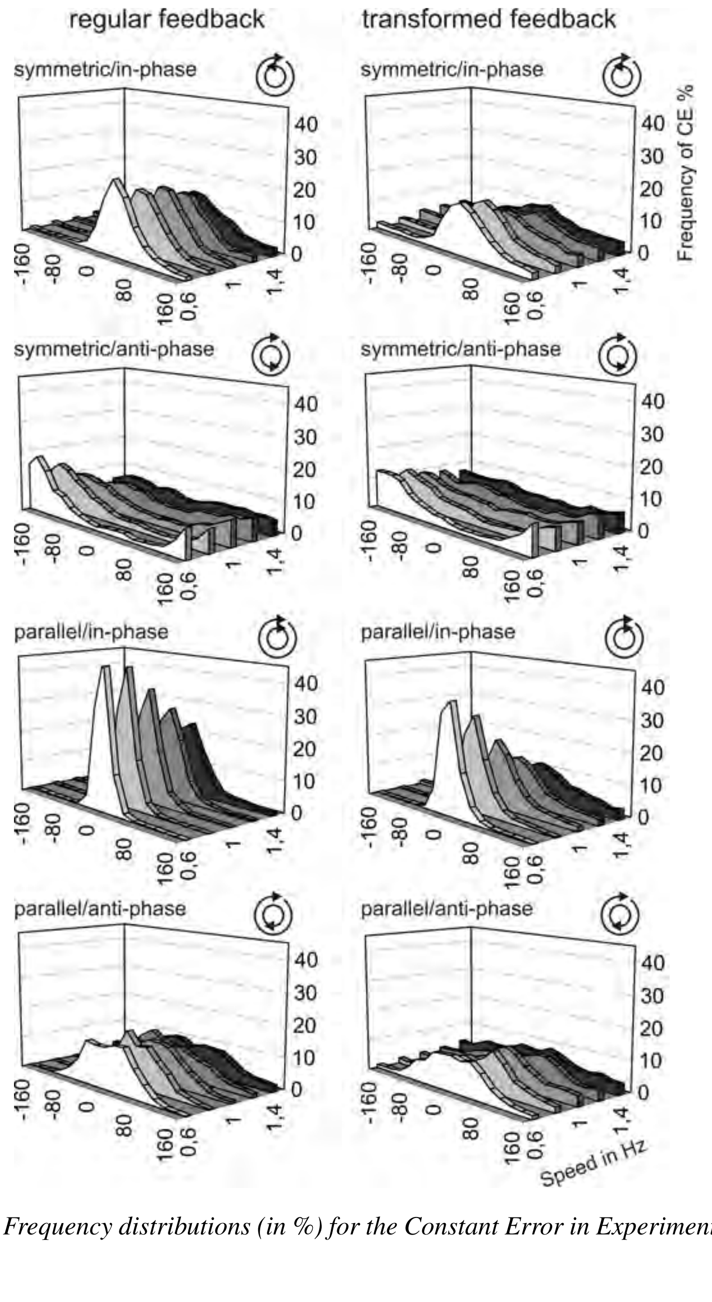

Figure 3.5: Frequency distributions (in %) for the Constant Error in Experiment 2 by speed level.

Instructed Mode (IM) and Contrary to Instructed Mode (CM)

As can be seen in Figure 3.5, participants produced the coordination patterns as instructed in all conditions but symmetry/anti-phase. In the symmetry/anti-phase trials, participants predominantly were in the CM. The pattern of performance was similar in the transformed feedback trials, although accuracy was slightly lower. These observations were confirmed by an ANOVA on IM.

There was a significant main effect of Speed, $F(4,60)=21.5$, $p<0.001$, showing that the time participants spent in the mode instructed decreased with higher speed levels. This effect was more pronounced in in-phase than in anti-phase trials, indicated by a significant interaction of Speed x Phase, $F(4, 50)=15.2$, $p<0.001$. This is probably due to a floor effect, as performance in anti-phase trials was already worse, thus leaving less space for deterioration. There was also a significant interaction of Rotation x Speed, $F(4,60)=30.6$, $p<0.001$, showing stronger effects of speed on parallel trials compared to symmetric trials, and an interaction of Feedback x Speed, $F(4,60)=5.2$, $p=0.001$, showing stronger effect of speed on transformed feedback trials compared to regular feedback trials. There was a significant main effect of Feedback, $F(1,15)=25.4$, $p<0.001$, showing that participants spent less time in the instructed mode with transformed feedback compared to regular feedback. A significant interaction of Phase x Feedback, $F(1,15)=11.\ 9$, $p=0.004$, reflects that this effect was stronger for in-phase than for anti-phase trials. As performance in anti-phase trials was generally worse than in in-phase trials this might be a floor effect. There was a significant interaction of Feedback x Rotation, $F(1,15)=26.4$, $p<0.001$, showing that feedback had little effect on symmetric conditions, $t(15)=1.9$, but performance in parallel trials suffered from transformed feedback, $t(15)=5.7$, $p<0.001$. There was also a significant main effect of Phase, $F(1,15)=133.4$, $p<0.001$, showing that participants spent more time in the instructed mode in in-phase conditions compared to anti-phase conditions. Because this is the case for regular feedback as well as for transformed feedback, this indicates that participants preferred the in-phase relation between stimulus and effect compared to the in-phase relation between stimulus and hand. There also was a significant main effect of Rotation, $F(1,15)=198.3$, $p<0.001$, showing that participants spent more time in the IM in parallel trials compared to symmetric trials.

To analyze CM, we performed one-sided t-tests to see whether participants were above chance in any of the conditions (condition data was combined over feedback). The symmetry/anti-phase condition was the only condition in which CM was significant above chance (see Table 3.2). Participants also spent more time in CM than in IM in this condition, $t(15)=5.6$, $p<0.001$.

Constant Error (CE)

A repeated measures analysis with the factors Feedback (regular, transformed), Condition (symmetry/in-phase, parallel/in-phase, parallel/anti-phase) and Speed (0.6 Hz, 0.8 Hz, 1 Hz, 1.2 Hz, 1.4 Hz) was conducted on CE. Note that we only included the conditions that were steadily performed by the participants, i.e. IM better than chance. There were no negative values for any of the conditions analyzed (see Table 3.2). There was a main effect of condition, $F(2,30)=171.4$, $p<0.001$, showing that there were no differences in CE for the parallel conditions ($t(15)=-1.1$) but higher CE for the symmetric/in-phase condition. A significant interaction of Feedback x Condition, $F(2,30)=10.6$, $p=0.005$, showed that transformed feedback had no effect on the parallel conditions but reduced the CE in the symmetric/in-phase condition.

Variable Error (VE)

A repeated measures ANOVA with the factors Condition (symmetry/in-phase, parallel/ in-phase, parallel/anti-phase), Feedback (regular, transformed), Location (24 sections, each covering 15 degrees of the trajectory), and Speed (0.6 Hz, 0.8 Hz, 1 Hz, 1.2 Hz, 1.4 Hz) was conducted on VE. Condition symmetry/anti-phase was excluded from this analysis because it was not successfully performed by the participants. We found the same pattern of results as in the error analysis, i.e. participants' variability increased with speed, they were more variable with transformed feedback and were least variable in parallel/in-phase trials compared to symmetry/in-phase and parallel/anti-phase trials as is evident from main effects for Speed, $F(4,60)=62$, $p<0.001$, Feedback, $F(1,15)=38.8$, $p<0.001$ and Condition, $F(2,30)=21.6$, $p<0.001$.

There was a significant interaction of Location x Condition x Feedback, $F(46, 690)= 6$, $p<0.001$, showing that symmetry/in-phase was the condition that showed strongest differences of VE between the locations and that the preferred location was modulated by transformed feedback (See Figure 3.6). While symmetric tri-

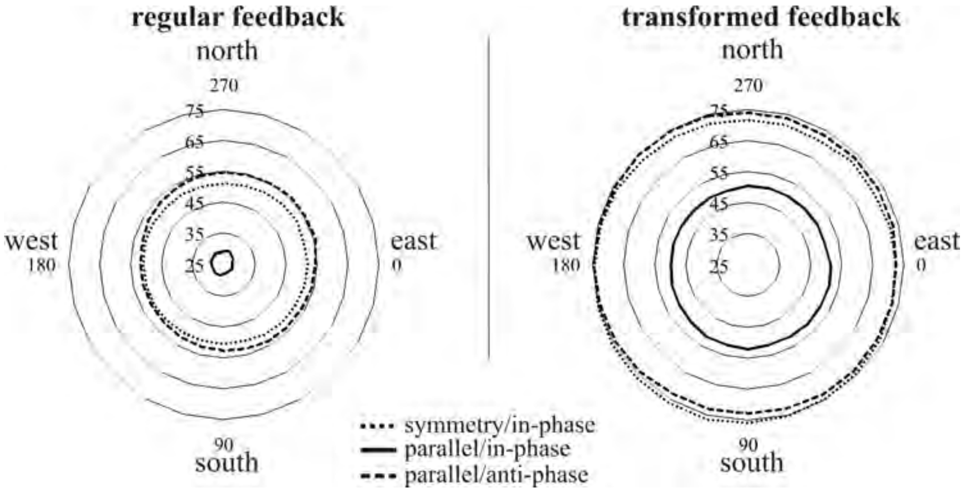

Figure 3.6: The distribution of the VE along the circular trajectory for the three analyzed conditions with regular and transformed feedback.

als benefit from South and West with regular feedback, they benefit from East and North with transformed feedback. Parallel/in-phase trials show a clockwise increase of VE with lowest values at east position with regular feedback, but a clockwise decrease of VE for transformed feedback. Parallel/anti-phase trials show a benefit for locations South and West with regular feedback, but benefit from locations East and South with transformed feedback. However, these effects are small in comparison to the main effects from the error analysis.

3.3.3 Discussion

In Experiment 2 participants performed unimanual continuous circling movements which varied in rotation (symmetric, parallel), and phase (in-phase, anti-phase) relative to a circling stimulus dot. Further, feedback of the movement was either regular or transformed by a 180°phase shift. In contrast to Experiment 1, in which stimulus and effect dot were presented to the left and the right of the body midline, stimulus and effect dot were presented on interleaved trajectories in Experiment 2. Overall, performance resembled Experiment 1. The data pattern for regular and transformed feedback conditions was similar, indicating that coordination was based on the effect-to-stimulus relation but not on the movement-to-stimulus relation. Again we found better performance for in-phase conditions than for anti-phase conditions, and again participants were not able to perform according to the instructions in the symmetry/anti-phase condition. Instead, they fell into symmetry/in-phase (defined in terms of the visual pattern), regardless of whether the movement was regular or transformed. Anchoring locations varied between conditions and were modulated by feedback.

In contrast to Experiment 1, performance in the error rates for the parallel/in-phase condition was better than in the symmetry/in-phase condition. This indicates that the manipulation of the visual setup was successful in changing the relative difficulty of the coordinative patterns and shows that the visual setup of a task indeed has an influence on unimanual coordination with external events. The distance between the two dots changed constantly in the symmetric conditions whereas in the parallel conditions the distance of the dots was constant. Even though those movement characteristics are the same for experiment 1, the closeness of the trajectories in experiment 2 highlights the differences between symmetric and parallel movement patterns even more. A perceptual explanation why the latter pattern is easier to perform is offered by the Gestalt laws of perceptual organization. These principles describe certain patterns of organization that are preferred in visual perception (Metzger, 1954). Some of these principles apply to the visual patterns in the present experiment, resulting in easier control of certain perceptual patterns. The principle of common fate (Wertheimer, 1923), which means that objects moving in same direction are perceived as belonging together, may play a role in both parallel conditions. Additionally, the principle of proximity, which means that objects that are close together are seen as belonging together can be applied to parallel/in-phase condition. There is experimental evidence showing that participants prefer to perceive movement patterns that are in accordance with the Gestalt laws of proximity and common fate (Börjesson & Ahlström, 1993; ?, ?). and that an 'isodirectional gestalt' facilitates spatial complex movement patterns (Bogaerts et al., 2003). Of the four instructed patterns the simplest according to Gestalt criteria is parallel/in-phase and indeed participants show the best performance in this condition.

Another piece of evidence on how much our new visual setup highlights the differences between the four movement patterns comes from our anchoring analysis. Location north is no longer beneficial for all conditions like it was in experiment 1. Instead preferred locations change between instructed movement patterns and with feedback. We have to consider the fact that anchoring is movement related. This is most obvious for symmetry/in-phase conditions where participants use the hand positions south and west for anchoring[3]. For the other conditions the relation is not so clear, still the fact that there is a divergence between regular feedback trials and transfered feedback trials means that anchoring can not be exclusively based on visual processes.

3.4 Experiment 3

In Experiment 2 the relative difficulty of the coordinative patterns was successfully changed by manipulating the visual-spatial setup of the task. In the third experiment we used yet another visual setup of the stimulus-effect relation: the trajectory of the stimulus and the trajectory of the effect dot were presented vertically aligned, i.e. the circles were presented above each other. The same feedback and rotation conditions as in the previous experiments were conducted. However, instead of stimulus and effect moving on a horizontal line for in-phase conditions it was now required that they move on the same vertical line (see Figure 7).

We expected to replicate the previous effects that performance patterns are similar under regular and transformed feedback. We had no specific hypothesis about the symmetric and parallel patterns in this experiment. However, we expected a similar benefit for aligned conditions as for the in-phase conditions in the previous experiments. Again we expected that the effect dot is in advance of the stimulus dot.

3.4.1 Method

Participants

Sixteen adults (nine female and seven male, aged 22 to 31) were paid seven Euros/hour to participate in single sessions.

Apparatus and Stimuli

The centers of the dots' trajectories were aligned on the vertical midline of the screen. The center of the upper trajectory was 150 pixels from the upper edge of the

[3]With transformed feedback hand positions south and west equal locations north and east.

screen, and the center of the lower trajectory was 450 pixels from the upper edge of the screen. This resulted in a distance of 300 pixels between the two centers. The positions of stimulus and effect trajectory were randomized between participants. Because performance had deteriorated with faster speed in both of the previous experiments, we only conducted the five speed levels which were eventually analyzed here (0.6 Hz, 0.8 Hz, 1.0 Hz, 1.2 Hz, 1.4 Hz) in the present experiment. Effective testing time was 44 minutes.

Procedure and design

Due to the vertical arrangement of the trajectories keeping the same distance from location south for both dots did not have the same visual grouping effect as in the previous experiments. We instructed participants on movement rotation with the stimulus (i.e. parallel) and contrary to the stimulus (i.e. symmetry) and regarding factor phase they where told to keep the dots at the 'same' position at the x-axis or 'shifted' which means 180° from the 'same position[4]. For reasons of comparability with the other experiments we decided to rename and reorganize our conditions and distinguish between same movement direction on the y- axis which will be referred to as y-in and different movement direction on the y-axis which will be referred to as y-anti (see Figure 3.7). In this experiment we conducted a short interview after the task, in which participants were asked whether they had noticed the transformation, whether their strategies differed for regular and transformed trials, and how they evaluated their performance.

Data analysis

Preliminary analysis showed that there were no differences in the error data patterns with respect to the positions (top or bottom) of the effect trajectory, therefore the data were combined. However, for the anchoring analysis we included a group factor.

[4]In German the instructions would be 'Mit' for 'with the stimulus'; 'Entgegen' for 'contrary to the stimulus'; 'Gleich' for 'same' and 'Versetzt' for 'shifted'.

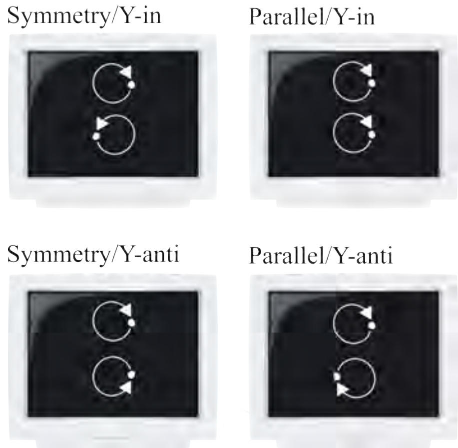

Figure 3.7: Illustration of the four instructed patterns for Experiment 3. Circles symbolize position of stimulus dot or effect dot, arrows symbolize movement trajectory and direction.

3.4.2 Results

Figure 3.8 illustrates the results, the means and standard deviations (averaged across speed levels) for the dependent variables are given in Table 3.3.

	Regular feedback				Transformed feedback			
	Symmetric		Parallel		Symmetric		Parallel	
	Y-In	Y-Anti	Y-In	Y-Anti	Y-In	Y-Anti	Y-In	Y-Anti
	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)
Instructed Mode %	42 (18)	9 (18)	68 (20)	47 (17)	38 (16)	11 (15)	53 (19)	45 (15)
Contrary Mode %	16 (22)	60 (24)	5 (7)	8 (8)	17 (12)	53 (24)	8 (6)	9 (7)
Constant Error	4 (23)	*	14 (14)	18 (20)	3 (16)	*	10 (7)	21 (21)
Variable Error - east	57 (17)	*	29 (7)	54 (13)	58 (15)	*	52 (12)	57 (14)
Variable Error - south	66 (23)	*	35 (8)	61 (18)	75 (19)	*	64 (16)	70 (20)
Variable Error - west	68 (24)	*	35 (7)	61 (20)	72 (20)	*	62 (17)	69 (20)
Variable Error - north	67 (23)	*	34 (7)	61 (17)	71 (18)	*	71 (16)	67 (18)

*Table 3.3: Note. All values for IM and CM differed significantly from the expected value for random performance (25%), * those values cannot be interpreted in a straightforward way because participants' performance was not predominantly in the instructed mode.*

Instructed Mode (IM) and Contrary to Instructed Mode (CM)

As can be seen in Figure 3.8, participants show coordination patterns that comply with the instruction in all but the symmetry/y-anti condition. In the symmetry/y-

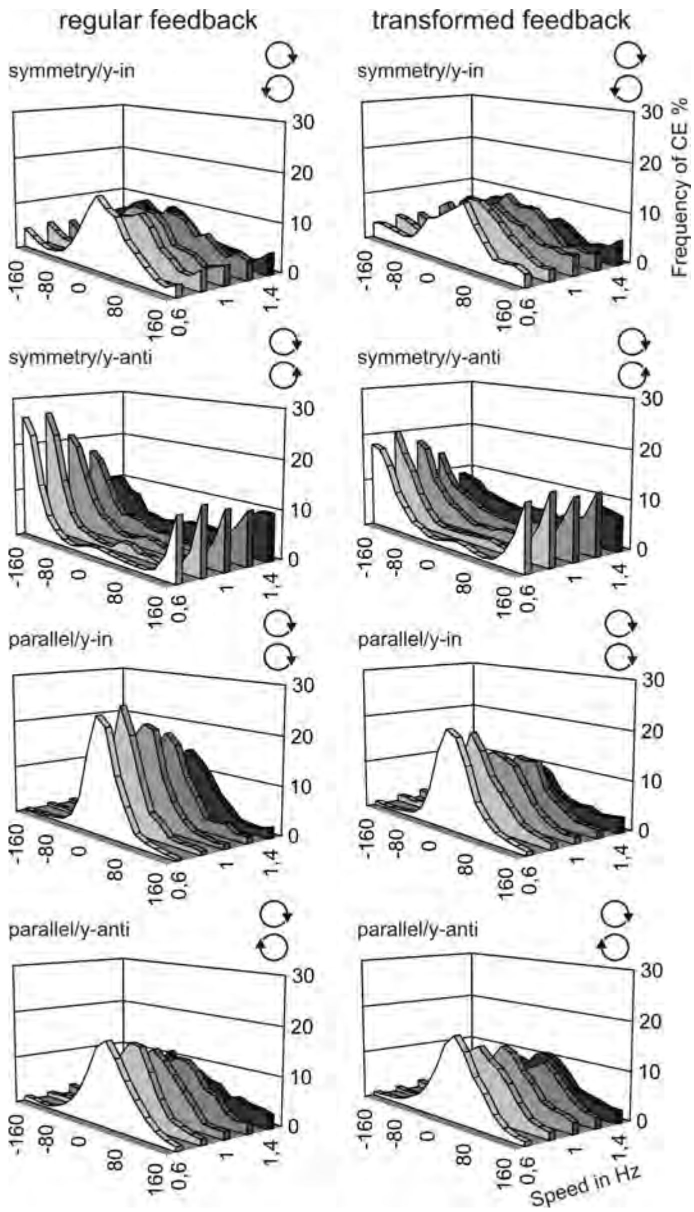

Figure 3.8: Frequency distributions (in %) for the Constant Error in Experiment 3 by speed level.

anti condition participants did not manage to execute the instructed pattern, but fell into the contrary to instructed pattern (i.e. symmetry/y-in). This was the case for both regular feedback trials and transformed feedback trials. There was a slight reduction in accuracy of performance with transformed feedback for all conditions. Those observations were confirmed by an ANOVA on IM.

The ANOVA showed that performance accuracy was a negative function of speed in a main effect for Speed, $F(4,60)=11$, $p<0.001$. There was a main effect of Feedback, $F(1,15)=6.8$, $p=0.02$, showing that IM decreased with transformed feedback compared to regular feedback. This effect is stronger for parallel and y-in conditions as interactions of Feedback x Rotation, $F(1,15)=10.1$, $p=0.006$, and Feedback x Phase, $F(1,15)=10.3$, $p=0.006$, show. Participants spent most time in the instructed mode with parallel/y-in, followed by symmetry/y-in and parallel/y-anti, which did not differ in IM, $t(15)=-1.2$, and showed lowest IM in symmetry/y-anti trials as can be seen from a significant interaction Rotation x Phase, $F(1,15)=5.6$, $p=0.032$.

To analyze CM, we performed one-sided t-tests to test whether participants were above chance in any of the conditions (condition data was combined over feedback). This was the case in the symmetry/y-anti condition, $t(15)=5.4$, $p<0.001$. They also spent more time in CM than in IM in this condition, $t(15)=4.6$, $p<0.001$.

Constant Error (CE)

To analyze CE, we only included those conditions that were performed according to instructions by the participants i.e. IM was better than chance. A repeated measures analysis with the factors Feedback (regular, transformed), Condition (symmetry/out-of-line, parallel/in-line, parallel/out-of-line) and Speed (0.6 Hz, 0.8 Hz, 1 Hz, 1.2 Hz, 1.4 Hz) was conducted on CE. There were no negative values in any of the analyzed conditions, for means see Table 3. There was a main effect of speed, $F(4,60)=22.2$, $p<0.001$, showing that the distance by which the participants were ahead of their supposed position decreased with increasing speed. There was a main effect of condition, $F(2,30)=8.3$, $p=0.001$, showing smallest CE values for symmetric/out-of-line conditions. In fact those values were not significantly different from zero ($t(15)=0.8$). There was no difference between the values for the parallel conditions, $t(15)=-2.1$.

Variable Error (VE)

A repeated measures ANOVA with the within subject factors Condition (symmetry/y-in, parallel/y-in,parallel/y-anti), Feedback (regular, transformed), Location (24 sections, each covering 15 degrees of the trajectory), and Speed (0.6 Hz, 0.8 Hz, 1 Hz, 1.2 Hz, 1.4 Hz) and between subject factor group (upper circle, lower circle) was conducted on VE. Condition symmetry/in-line was excluded form this analysis because participants did not perform above chance in measure IM. There was no main effect for group i.e. there was no difference in general performance variability depending on whether the effect moved on the upper or lower trajectory. Participants showed greater VE with transformed feedback, variability increased as a function of speed and participants showed lower VE for the parallel conditions compared to symmetric/out-of-line condition as shown by main effects of Feedback(1,14)=6.9, p=0.02, Speed, F(4,56)=16.5, p<0.001, and Condition, F(2,28)=51.9, p<0.001.

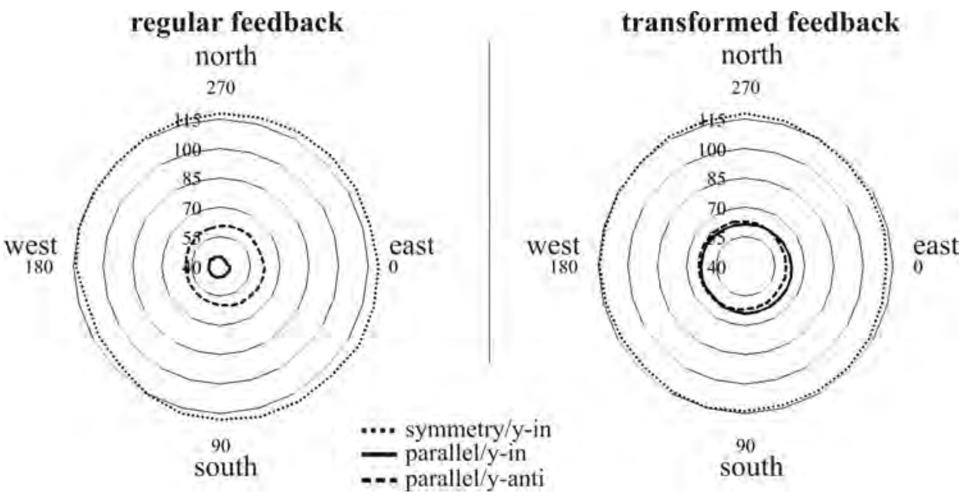

Figure 3.9: The distribution of the VE along the circular trajectory for the three analyzed conditions with regular and transformed feedback.

There was an interaction of Location x Condition x Feedback, F(46,690)=3.7, p=0.014, showing a benefit for symmetry/y-in trials at location west that disappears with transformed feedback (see Figure 3.9. An interaction Section x Condition x Group shows that this effect is mainly based on the performance of the group with the effect dot on the upper circle. We find a reversion of anchoring patterns for the parallel trials with transformed feedback. Parallel/y-in performace benefits from

East and South location with regular feedback but from West and North location with transformed feedback. Parallel/y-anti conditions benefit from location West with regular feedback but from East and South with transformed feedback. Those differences in anchoring dependent on feedback show that anchoring in contrast to general task performance is movement related.

Questionnaire Data

Of the 16 participants none reported to have used different strategies in the regular and transformed feedback trials. Four participants evaluated their performance worse with transformed feedback compared to regular feedback, whereas the other twelve thought they had not performed any different under both feedback conditions. 7 of those 12 participants reported not to have noticed the transformation at all.

3.4.3 Discussion

In Experiment 3 participants performed unimanual continuous circling movements which varied in rotation (symmetry, parallel), feedback (regular, transformed), and phase (y-in, y-anti). In contrast to the previous experiments, the stimulus dot and effect dot were presented on vertically aligned trajectories. Again, the data patterns for regular and transformed feedback conditions were similar, indicating that coordination was based on effect-to-stimulus-coordination but not on movement-to-stimulus-coordination. Performance in the conditions resembled that in experiment 2, with best performance in parallel/y-in conditions, intermediate performance in symmetry/y-in and parallel/y-anti conditions and worst performance in symmetry/y-anti conditions. Anchoring varied between conditions and was modulated by feedback.

Against our expectations, vertical alignment did not offer a comparable benefit as the horizontal alignment which comes along with in-phase movement patterns. If this had been the case we should have found a benefit for symmetry/y-anti compared to symmetry/y-in conditions. However, regarding our previous considerations on movement direction in reference to the body the results of this experiment fit in nicely. We find that moving towards and away from the body synchronously is more beneficial than vertical alignment.

We can only speculate about what makes vertical alignment different from horizontal al alignment. It may be that the vertical and the horizontal dimension differ in terms of how they are perceived and how vertical and horizontal stimuli are processed. Research indicates that people are more familiar with making left-right distinctions than up-down distinctions (Nicoletti & Umilta, 1989). Further, in the vertical-horizontal illusion, a vertical line gets misjudged as longer as a horizontal line of the same size (Künnapas, 1955). The illusion is explained by properties of humans' visual field which has an elliptic form (Prinzmetal & Gettleman, 1993). A vertical line is consequently nearer to the edge of the visual field than a horizontal line of the same length. The same is the case for the stimuli arrangement in experiment 3 compared to 1, even though the physical distances were the same. The difficulty with the vertical display may have been further enhanced by the shape of the computer monitor, which is wider than it is high. There are two conditions in which the dots have to take positions that have the maximum possible vertical distance: the parallel/y-anti and symmetry/y-anti condition. Participants show worse results in those conditions than in conditions with same rotation but opposite phase instruction. However, even though the difficulty of the vertical display probably gives rise to the observed effects, the data pattern cannot be explained by the difficulty of conditions alone.

There was a no influence of location on symmetry/y-in trials which might be due to a ceiling effect. Even with potentally helpful salient locations this conditions is very demanding. This could again be explained by the different directions of effect and stimulus in reference to the body. We can also draw on this hypothesis to explain the results for the parallel trials. When the hand and the stimulus move towards and away from the body synchronously, which is the case with regular feedback for parallel/y-in, with transformed feedback for parallel/y-anti, participants benefit from locations East and South. If hand and stimulus do not move towards and away from the body synchronously, which is the case with regular feedback for parallel/y-anti, with transformed feedback for parallel/y-in, they benefit from locations West and North. It seems that anchoring phenomena are strongly influenced by the relation between stimulus and hand.

One may wonder whether the fact that participants performed the task slightly to the right of the body midline plays a role for the observed data. A perceived mismatch between hand position and effect position may lead to the use of a horizontal representation. We had done this, because it was more convenient for participants to perform the movements at the right of the body midline instead of at the body midline and to keep the movement constant between experiments. However, we conducted a control experiment, in which the center of the hand movement trajectory was aligned with the center of the stimulus and the body midline (data not reported). We obtained the same pattern of results as in Experiment 3. Nevertheless, it could still be that simply using a limb which is by necessity located on one side of the body leads to changed representation of vertical displays under certain conditions, regardless of the actual movement position, which in probably not represented very accurately (Frith, Blakemore, & Wolpert, 2000; Fourneret & Jeannerod, 1998).

To sum up, the results of Experiment 3 again indicate that unimanual coordination occurs between stimulus and effect rather than between the stimulus and the movement. Shared direction in reference to the body is more beneficial than vertical alignment.

3.5 General Discussion Part I

To investigate action-to-event coordination we used an unimanual circling task. Trajectories of stimulus and effect were either presented horizontally aligned, interleaved or vertically aligned. Participants were instructed to maintain one of four movement patterns that were defined by rotation and movement phase. To distinguish between the role of effect-to-stimulus-coordination and movement-to-stimulus-coordination, we dissociated movements and effects by means of transformed feedback. The error data from all three experiments indicated that coordination was based on effect-to-stimulus-coordination rather than movement-to-stimulus-coordination, as there were no differences in the performance patterns between regular and transformed feedback conditions. The different visual setups in the experiments modified the relative level of difficulty of the different conditions. In all experiments, the movement effect was in advance of the stimulus dot in all conditions that were performed predominantly in the instructed mode. Anchoring was dependent on visual setup, condition and feedback mode and was sensitive to task difficulty.

Our results on how the actual movement contributes to coordination of this task are mixed. From the error analysis we get evidence that action-to-event-coordination is realized in terms of stimulus-to-effect-coordination. This is supported by the observation that in-phase relations between effect an stimulus are more beneficial for performance than in-phase relations between hand and stimulus. Does this mean that the hand movement is irrelevant as long as the visual effect forms a 'good gestalt' - end of story? Our results provide evidence that this is not the case. For one thing we have costs in terms of poorer performance whenever the hand and the visual effect are dissociated by a transformation. This is accounted for by other studies (Lepper, Massen, & Prinz, 2008; Roerdink et al., 2005), however those costs might be reduced by extensive training. We find smaller differences between visual in-phase and visual anti-phase for transformed feedback conditions compared to regular feedback conditions. This could indicate a subtle effect of the hand rotation. As this effect mainly stems from a decrease in in-phase performance with transformed feedback it is also possible that this only reflects the effect of the transformation. In our anchoring results, for two of our experiments we find, that the location used for anchoring change with transformed feedback, which can not be explained by the visual input and the stimulus-effect-relation as they are not affected by the feedback manipulation.

Shared movement direction in reference to the body seems to be a key determinant of performance quality in our paradigm. In the absence of other landmarks on the trajectory, like turning points in oscillation movements, participants use this characteristic to subdived their movements. This is also the explanation why participants use location north for anchoring in experiment 1. With the conditions being quite similar in the standard setup participants used the location where movement direction in reference to the body changes. However, direction in reference to the body is only one of the features to determine performance accuracy. It can only hint the to be expected difficulty of the movement but but can not predict performance quality completely. An example for this from Experiment 3 is performance in symmetry/y-in and parallel/y-anti conditions. Participants show the same level of performance quality although movement direction in reference to the body is the same for symmetry/y-in but different for parallel/y-anti between stimulus and effect. This concept might be predominantly visual as patterns do not change with feedback.

The questionnaire results from Experiment 3 indicate that most participants were not aware of the transformation while performing the task. While the presence of the transformation slightly reduced performance, few of the participants reported any difficulties with the transformation after the experiment. Evidence from other studies indicates that participants are not very good in knowing their actual hand positions in similar tasks (Frith et al., 2000; Fourneret & Jeannerod, 1998). This 'visual dominance' might be based on the fact that there is less noise in the visual domain and that visual feedback is more easily accessible in some tasks (Wilson, Collins, & Bingham, 2005b, 2005a). In our case participants most likely represented the position of the hand not where it actually was but where the visual effect indicated it to be.

In none of the experiments an advantage of mirror symmetric in comparison to parallel movements was observed. In the contrary, we find evidence that symmetric tracking is harder than parallel tracking. One piece of evidence comes from the fact that we find switches from instructed anti-phase patterns to in-phase patterns only for symmetric trials. More evidence comes from strong use of anchoring and lower accuracy of symmetric compared to parallel conditions. This speaks against perceived symmetry as a general beneficial concept at least for unimanual coordination. This is in contrast to bimanual studies, in which mirror-symmetric movements are generally associated with better and more stable performance (Mechsner et al., 2001; Swinnen, Jardin, et al., 1997, e.g.). One explanation might be that in bimanual studies indeed the coactivation of homologous muscles (Swinnen, Jardin, et al., 1997; Kelso, 1984) or the specification of equal parameters for both limbs (Oliveira, 2002; Heuer, 1993) does play a role for the observed symmetry effect. This is something which does not occur in unimanual coordination, and from a perceptual perspective symmetric and parallel patterns may be of equal difficulty (as in Experiment 1). In fact, by manipulating the display we were even able to show better performance in parallel patterns than in symmetric patterns (Experiment 2 and 3). There is one previous unimanual study showing that participants prefer parallel motions compared to symmetric motions when they only have visual feedback i.e. they have to rely on the representation of the movement (Alaerts et al., 2007). Participants had to coordinate the movement of their right hand either to the movement of a dummy hand (vision condition) or their passively moved left hand while being blindfolded (proprioception condition). If participants had to rely on proprioceptive feedback they performed better in mirror symmetric movements. These observations fit in well with the present results especially for Experiments 2 and 3.

Of course, participants always had both visual and proprioceptive feedback in the present experiments, but as they relied more on the visual effects of the movements a preference for parallel movements is plausible.

The visual setup had a significant impact on the relative difficulty of the different coordination patterns. Together with the results from the feedback manipulation this supports our conclusion that action-to-effect coordination functions as effect-to-stimulus- coordination. Participants performed best in those conditions in which the pattern of the effect and the stimulus forms the easiest and most stable Gestalt (see also (Bogaerts et al., 2003; Mechsner, 2003)). In those conditions participants probably grouped the stimulus and the effect dot in order to monitor performance in accordance with the Gestalt principles.

Participants showed a positive bias in their CE-values in all conditions and all experiments, meaning that they were ahead of their ideal position. We interpret this as a mechanism similar to the negative asynchrony known from tapping studies. When asked to synchronize with a metronome participants usually tap slightly too early. This is explained by a central representation that combines auditive and somatiosensory feedback. In order to coincide at that central level the tap has to be executed before the auditory cue. The cause for this delays are different conduction times along afferent pathways (?, ?).

In conclusion, action-to-event coordination takes place between the stimulus and the movement effects rather than between the stimulus and the movement itself. An egocentric Frame of Reference (FoR) is active in unimanual coordination resulting in a benefit for situations where stimulus and effect move towards and away from the body synchronously.

Chapter 4

Part II - Transformations

4.1 Introduction

On August 16th 2008 millions of people watched astonished as Jamaican athlete Usain Bolt improved his own world record in the 100m mens finals of the Olympic games in Beijing. His incredible speed even allowed him to slow down on the last 20m and celebrate his victory. How fast can this man go, audience all around the world asked themselves. How fast can men go, anyway? Average peoples running speed is about 11.5 km/h (Bramble & Lieberman, 2004). Usain Bolt reached 44 km/h. The speed limit in German cities is at 50 km/h, a velocity a average human will never reach on foot and even highly trained athletes can only sustain for seconds. What does it mean for our coordinative abilities that we navigate most of the times at speeds our own body could not produce? How do we deal with dissociations between motor and visual speed? This is one of the questions we will focus on in this part of the dissertation.

A characteristic of machines like cars and other tools which allows us to overcome motor system limitations is that their use implies the existence of a transformation between bodily movements and the resulting consequences in external space. People are usually able to adapt quite well to such transformations (Imamizu et al., 2000; Ghahramani, Wolpert, & Jordan, 1996; Kagerer, Contreras-Vidal, & Stelmach, 1997; Wolpert, Ghahramani, & Jordan, 1995), although some transformations are easier to learn than others. In a study by Mohler, Thompson, Creem-Regehr, Pick Jr, and Warren Jr (2007) participants were walking on a treadmill and received visual input of half, twice, or the same speed as walking speed. Preferred walking speed was lower with doubled visual speed and higher with halved visual speed compared to when visual and walking speed were the same. When motor and visual speed were dissociated, participants chose a walking speed that would bring visual speed closer to their preferred speed if they were connected. Similar results have been obtained in unimanual hand movement studies. Movements are more difficult with higher gains, resulting in a deterioration in accuracy when movement frequency is given (Rosenbaum & Gregory, 2002), or in slower movements when participants are free to choose their movement speed (Rieger et al., 2005). Presumably, those adjustments reflect that the cognitive system tries to maximize the predictability of the perceived trajectory.

In general, transformations scaling gain are easy to adapt to (Bedford, 1994; Bock & Burghoff, 1997; Seidler, Bloomberg, & Stelmach, 2001; Rieger et al., 2005), whereas transformations involving nonlinear relationships are more difficult to acquire (Heuer & Hegele, 2007; Rieger, Verwey, & Massen, 2008; Verwey & Heuer, 2007). The transformation itself seems to be an important part of the cognitive representation of tool-use actions (Massen & Prinz, 2007; Lepper et al., 2008). Transformations can scale up the effect relative to the movement, as in driving a car, but they can also scale down the effect relative to the movement, as in using a lever with a pivotal point close to the effect side.

In this second part of the dissertation we will try to meet the need to study the sensitivity of motion planning to parameters of the visuomotor transformation (Flanagan & Rao, 1995, p.2177). Participants were exposed to phase shifts (Experiment 4) and gain transformations (Experiment 6) of different magnitude and a reversion of rotation transformation (Experiment 5). We wanted to investigate systematically how different visuomotor transformation affect performance if the visual input and the actual hand movement are kept constant.

4.2 Experiment 4 - Phase Shifts

4.2.1 Introduction

So far we used phase shifts of 180° which reverse the phase relations between hand and stimulus and effect and stimulus. To take a closer look at the perceptual-motor mechanisms involved in coordination we needed an experiment with a more gradual manipulation of the distance between movement and effect. Here we used four positive phase shifts (45°, 90°, 135°, 180°) and three negative phase shifts (-45°, -90°, 135°). All conditions were also performed with regular feedback. We know from coordination studies that in-phase (phase shift 0°) and anti-phase (phase shift 180°) are the two most stable coordination modes (Haken et al., 1985). From previous experiments we know that phase shifts of 180° impair coordination performance. Phase shifts of 180° between hand movement and visual effect reverse the movement direction relative to the body between hand movement and visual effect. This means that with in-phase instruction stimulus and visual effect move away from the body, while the hand moves towards the body and vice versa. With anti-phase instruction stimulus and hand share the same movement direction in reference to the body i.e. hand and stimulus move away from the body, while the visual effect moves towards the body and vice versa. As we found in the previous experiments, shared movement direction in reference to the body is a determining factor for coordination quality. If our assumptions regarding the importance of movement direction in reference to the body are right, we should find best performance for 0°and 180°as the relation between hand and visual effect are univocal in those cases, i.e. the same or reversed. With phase shifts smaller than 180°the relation of the movement directions in reference to the body between hand and visual effect gets more ambiguous. This might result in higher variability and less accuracy in participants' performances. There are studies showing that coordination modes with 90° of phase shift are more difficult than with 180° of phase shift (Wilson et al., 2005a). The authors explain this effect with higher perceived variability of the 90°mode compared to 0° or 180°. They also found that a visual phase of 0° helped participants to stabilize movements that held a cross-modal phase of 90° and 180°.

4.2.2 Methods

Participants

Sixteen participants (seven male and nine female, aged 20 to 39 years, mean 25.6 years, SD 3.6 years) participated in a single session.

Procedure and design

Cross modal relation between hand and visual effect was manipulated in eight steps. There was regular feedback with is equal to a phase shift of 0°, in separate blocks 45°, 90°, 135°, -135°, -90°, -45° and 180° were added to the recorded hand position before it was presented on the screen. There were three speed levels of 0.8, 1 and 1.2 Hz. Every trial lasted 30 seconds. The feedback conditions were blocked and the order of the blocks was randomized between participants. Each block consisted of 6 trials. Altogether the participants had to complete 192 trials. Effective testing time was 99.2 minutes, however the time it took participants to complete a session was about two and a quarter of an hour, there were variations, because participants had the opportunity to take breaks as long as they wished to between the trials.

4.2.3 Results

We conducted repeated measures ANOVAs with the factors Phase Shift (-135°, -90°, -45°,0°, 45°,90°,135°,180°), Rotation (symmetry, parallel), Phase (in-phase, anti-phase) and Speed (0.8 Hz, 1 Hz, 1.2 Hz). For the CE analysis factor Condition (symmetry/in-phase, parallel/in-phase, parallel/anti-phase) replaced factors Phase and Rotation.

The results of Experiment are depicted in figure 4.1.

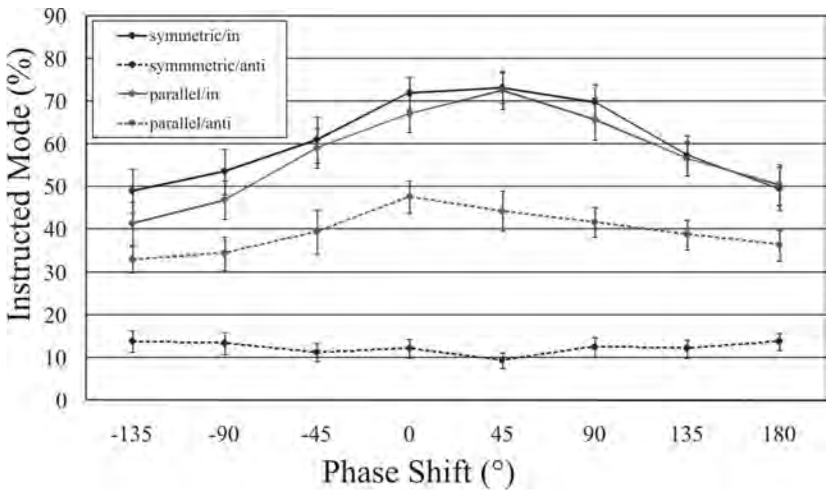

Figure 4.1: Depiction of the results for Instructed Mode in Experiment 4.

Instructed Mode

There was a significant main effect for phase shift, F(7,105)=36.7, p<0.001, showing more accurate performance with positive phase shifts compared to negative phase shifts. As expected participants were more accurate in in-phase conditions compared to anti-phase conditions as a significant main effect Phase, F(1,15)=86,6, p<0.001, shows. A significant interaction Phase Shift x Rotation x Phase, F(7,105)=3.1, p=0.005, shows bell shaped performance for the in phase conditions, with smaller decreases in performance for positive phase shifts compared to negative phase shifts and no difference in performance between symmetric and parallel rotations in in-phase conditions (for selected comparisons see Table 4.1 A). In in-phase conditions we find better performance for positive phase shifts compared to negative phase shifts of the same size (see Table 4.1 B). In anti-phase trials participants perform better in parallel conditions compared to symmetric conditions which fail to exceed chance level. In anti-phase trials the impact of increasing phase shift is weaker compared to in-phase conditions.

Contrary to Instructed Mode (CM)

To analyze CM, we performed one-sided t-tests to test whether participants were above chance in any of the conditions. This was the case for all phase shifts in the symmetry/anti-phase conditions (for test values see Table 4.2).

Constant Error

First of all the CE values were positive for all analyzed conditions, which means that participants always were ahead of their ideal position. There was a significant main effect of phase shift, F(7,105)=13.6, p<0.001, showing stronger lead with negative phase shifts. There was also a significant main effect of speed, F(2, 30)=42, p<0.001, showing smaller lead with higher speed.

Variable Error

Variability was lower for the in-phase conditions compared to parallel/anti-phase, as a main effect Condition, F(2,30)=33.3, p<0.001, shows. VE increased Speed, F(2,30)=29.5, p<0.001. There was a significant main effect of Location, F(23,345)=-

	Condition		Comparison		T-Value	P-Value
A	symmetry/in-phase	0°	vs	45°	-0.7	p=0.505
	symmetry/in-phase	45°	vs	90°	2	p=0.064
	symmetry/in-phase	0°	vs	-45°	3.8	p=0.002
	symmetry/in-phase	180°	vs	-135°	0.2	n.s
	parallel/in-phase	0°	vs	45°	-1.7	p=0.105
	parallel/in-phase	45°	vs	90°	2.4	p=0.028
	parallel/in-phase	0°	vs	-45°	3	p=0.008
	parallel/in-phase	-135°	vs	180°	-3.6	p=0.003
	parallel/anti-phase	180°	vs	-135°	1.1	n.s.
B	symmetry/in-phase	45°	vs	-45°	4.5	p<0.001
	symmetry/in-phase	90°	vs	-90°	5.6	p<0.002
	symmetry/in-phase	135°	vs	-135°	2.9	p=0.011
	parallel/in-phase	45°	vs	-45°	4.6	p<0.001
	parallel/in-phase	90°	vs	-90°	5	p<0.002
	parallel/in-phase	135°	vs	-135°	6.1	p<0.001

Table 4.1: Differences between phase shift steps for measure IM in Experiment 4. A) T-Test values for selected comparisons for Interaction Phase Shift x Rotation x Phase. B) Comparisons for negative and positive phase shifts, positive t-values indicate that performance was better for positive phase shifts compared to negative phase shifts.

Phase shift	Mean CM	T-Value	P-Value
-135°	35	4.7	p<0.001
-90°	36.9	3.6	p=0.003
-45°	38.6	3.5	p=0.003
0°	39.5	4.7	p<0.001
45°	45.1	6.4	p<0.001
90°	40.8	4.5	p<0.001
135°	38.8	5.2	p<0.001
180°	38.4	4.6	p<0.001

Table 4.2: Means and test values of symmetry/anti-phase conditions against chance for measure CM. Participants performed significantly better than chance, i.e. they actually produced symmetry/in-phase patterns.

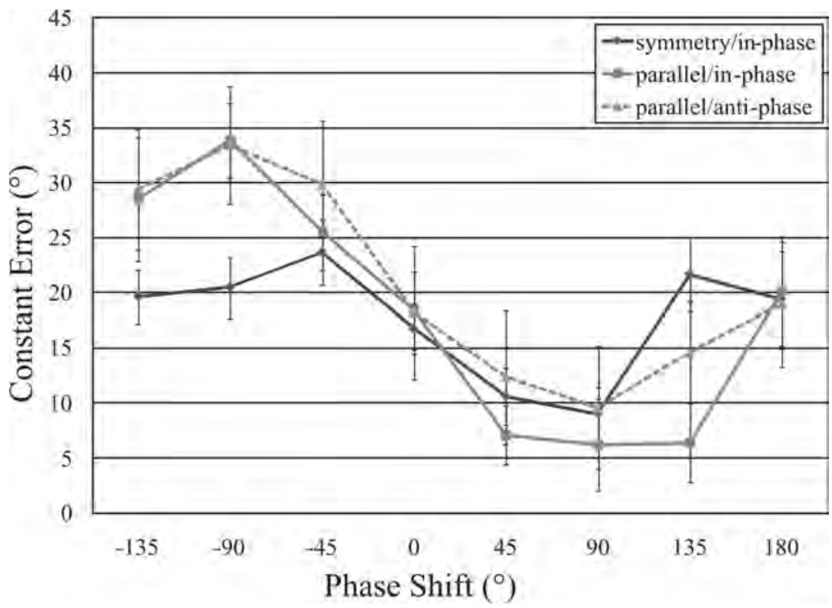

Figure 4.2: Depiction of measure Constant Error for Experiment 4.

14.8, $p<0.001$, showing that variability was lowest around location North and highest between locations South and West. This effect is strongest in symmetry/in-phase conditions, while parallel/in-phase conditions show only little variations in variability along the trajectory and it is more pronounced in bigger transformations (e.g. 180°compared to 45°) as can be seen in a significant interaction of Location x Feedback x Condition, $F(322, 4830)=2.8$, $p=0.003$.

Control Analysis

To control for effects of the CE distribution on IM we recalculated the IM using the mean CE of every participant for each Phase Shift +/- 45° as range. With the new values we run a repeated measures ANOVA with the factors Phase Shift (0°, 45°, 90°, 135°, 180°, -135°, -90°, -45°) x Direction (symmetric, parallel) x Phase (in-phase, anti-phase) x Speed (0.8 Hz, 1 Hz, 1.2 Hz). We find the same pattern of results meaning that the distribution of the CE-values had no impact on IM, i.e. our original analysis is valid. The results of the control analysis in detail: There was a significant main effect for Phase Shift $F(7, 105)= 11.7$, $p<0.001$, showing decreasing performance as phase shift nears 180°. There was a significant interaction of Direction x Phase, $F(1,15)=27.7$, $p< 0.001$, showing no differences in performance between the directions in in-phase conditions, but worse performance in symmetric/anti-phase compared to parallel/anti-phase condition. In-phase conditions were always performed more accurately than anti-phase conditions, $F(1,15)=258.7$, $p<0.001$.

4.2.4 Discussion

With this experiment we wanted to test the impact of transformation magnitude, in this case phase shifts, on coordination performance. We used our standard phase (in-phase, anti-phase) and rotation (symmetry, parallel) instructions and had participants perform with regular feedback and seven cross-modal phase shifts of different size (45°, 90°, 135°, 180°, -135°, -90°, -45°). Positive phase shifts evoked the perception of the effect leading the hand, while with negative phase shifts the effect seemed to trail behind the hand. Like in our previous experiments participants showed better performance in terms of accuracy in in-phase conditions compared to anti-phase conditions. Thus they benefit from simple visual feedback. The phase shifts have less effect on the anti-phase conditions, which might be due to a floor effect, especially for symmetry/anti-phase conditions where the time participants spent in the instructed coordination mode is below chance. Instead of performing the instructed anti-phase pattern participants switch into the in-phase mode in those conditions. Performance accuracy suffered with increasing phase shift. However, the perceptual consequences of the to be produces pattern interacted with phase shift in its effects on performance. We find a benefit for positive phase shifts, which we interpret as a benefit of perceived lead of the effect. For the in-phase conditions performance with regular feedback does not differ for performance with 45° phase-shift. The cause for this could be that participants confuse neighboring phases with 0° or 180° (Bingham, Zaal F.T.J.M., Shull, & Collins, 2001) however participants performance suffers from a negative phase shift of 45 degrees, which employs a physical displacement of the exact same size.

Our results for measure CE are a bit puzzling. Usually there is a clear cut positive bias for conditions were participants are more accurate and this bias declines with more difficult conditions or increasing speed (Experiment 1 to 3). Based on this knowledge we would expect higher CE values for positive phase shifts and a decline of the CE values with negative phase shifts. In our data however the opposite is the case. We have bigger positive bias with negative phase shifts compared to positive phase shifts. Maybe this reflects an overcompensation of participants perceiving the effect dot to lead the hand with positive phase shifts and and to lag behind the hand with negative phase shifts. It could be that participants try to make up for this lag by being more ahead. Our results suggest that there is a difference in the ability to coordinate the effect of our hand movement between those lag/lead conditions. Participants perform more accurate and produce less deviations with lead conditions even though the physical distance between the hand and the effect dot is the same e.g.. for phase shift 90° and -90°. In addition to the objective physical features of a transformation their subjectively perceived qualities are crucial for the way participants integrate it into the perception-action circle.

Phase Shift°			-135 M (SD)	-90 M (SD)	-45 M (SD)	0 M (SD)	45 M (SD)	90 M (SD)	135 M (SD)	180 M (SD)
symmetry	in-phase	IM %	61 (22)	54 (21)	49 (21)	72 (16)	73 (14)	70 (17)	57 (19)	49 (21)
	anti-phase	IM %	11 (8)	13 (10)	14 (10)	12 (9)	9 (7)	13 (9)	12 (8)	14 (8)
parallel	in-phase	IM %	59 (18)	47 (18)	41 (20)	67 (17)	73 (18)	66 (19)	57 (16)	50 (19)
	anti-phase	IM %	39 (21)	34 (15)	33 (12)	48 (15)	44 (19)	42 (14)	39 (14)	36 (14)
symmetry	in-phase	CM %	3 (6)	6 (8)	9 (10)	2 (4)	2 (3)	3 (6)	5 (5)	8 (9)
	anti-phase	CM %	39 (16)	37 (13)	35 (9)	39 (12)	45 (13)	41 (14)	39 (11)	38 (12)
parallel	in-phase	CM %	3 (2)	6 (6)	10 (7)	3 (3)	2 (2)	4 (7)	5 (6)	9 (7)
	anti-phase	CM %	12 (10)	14 (10)	14 (9)	7 (7)	10 (8)	12 (10)	14 (11)	13 (9)
symmetry	in-phase	CE°	24 (12)	20 (11)	20 (10)	17 (9)	11 (10)	9 (10)	22 (13)	19 (18)
	anti-phase	CE°	-36 (25)	-24 (24)	-24 (25)	-25 (32)	-18 (30)	-20 (22)	-13 (27)	-19 (31)
parallel	in-phase	CE°	26 (14)	34 (13)	29 (22)	18 (14)	7 (11)	6 (17)	6 (14)	20 (20)
	anti-phase	CE°	30 (23)	33 (21)	29 (22)	18 (24)	12 (24)	10 (22)	15 (18)	19 (23)

Table 4.3: Means and standard deviations for measure IM, CM and CE for Experiment 5.

4.3 Experiment 5 - Direction Reversion

4.3.1 Introduction

In Experiment 1 we found no differences between symmetric and parallel trials with in-phase instruction in terms of accuracy. Stronger influence of the phase manipulation on symmetric trials and the results of the anchoring analysis, however, indicate that there is a difference in task demands between parallel and symmetric trials. Our question was whether the reason for this difference was in the motor or visual properties of the respective movement direction. To be able to separate these two processes we decided to introduce a transformation that reversed the direction of the participants movement, i.e. symmetric hand movements resulted in parallel moving effects and vice versa. If the differences in performance were due to motor aspects of the movement direction we would expect reversed effects, i.e. better performance for instructed parallel /anti-phase compared to symmetry/anti-phase. If the differences in performance were due to visual factors the results should stay the same, showing impaired performance in symmetry/anti-phase trials compared to parallel/anti-phase trials. Based on our results from previous experiments we expected that overall performance would suffer in the transformed feedback trials. Second, we expected this effect to be stronger for the anti-phase trials compared to in-phase trials. In other words we expected an in-phase benefit to show itself in the regular as well as in the transformed trials. We expected stronger impact of increasing speed with transformed feedback. With our transformation movement direction in reference to the body stayed the same between hand and visual effect. As we found this movement characteristic a determining factor of coordination performance and our previous transformations always resulted in incongruent movement directions in reference to the body between hand hand visual effect we expected that participant might be able to cope better with this transformations than with the phase shift from experiment 1.

4.3.2 Method

Participants

Sixteen participants (five male and eleven female, aged 19 to 29 years, mean 23.6 years, SD 3 years) participated in a single session.

Procedure and design

For half of the trials the feedback was manipulated by a mirroring of the hand position at the vertical axis through the circular trajectory. This resulted in opposite movement direction between effect and hand, i.e. visual symmetry goes along with parallel movements and vice versa.

4.3.3 Results

We conducted repeated measures ANOVAs with the factors Rotation (symmetry, parallel), Phase (in-phase, anti-phase) and feedback (reguar, transformed).

The results are graphically depicted in Figure 4.3, the means and standard deviations (averaged across speed levels) for the different dependent variables are given in Table 4.4.

	Regular feedback				Transformed feedback			
	Symmetric		Parallel		Symmetric		Parallel	
	In-Phase	Anti-Phase	In-Phase	Anti-Phase	In-Phase	Anti-Phase	In-Phase	Anti-Phase
	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)
Instructed Mode %	48 (14)	19 (7)	48 (16)	35 (9)	25 (7)	25 (8)	25 (8)	27 (7)
Contrary Mode %	10 (5)	31 (11)	9 (7)	16 (5)	27 (7)	27 (7)	26 (7)	25 (7)
Constant Error	13 (10)	-10 (18)	18 (9)	18 (12)	-4 (13)	-3 (11)	-4 (11)	-3 (14)

*Table 4.4: Note. All values for IM and CM differed significantly from the expected value for random performance (25%), * those values cannot be interpreted in a straightforward way because participants' performance was not predominantly in the instructed mode.*

Instructed Mode (IM)

A significant interaction Feedback x Rotation x Phase, F(1,15)=14.6, p=0.002, shows the usual pattern of results for our four conditions with best performance in the in-phase conditions and worst performance in the symmetry/anti-phase condition which does not exceed chance (t(15)=-3.2, p=0.006). With transformed feedback, however, all conditions are at chance level.

Contrary Mode (CM)

We performed one-sided T-Test to check whether any of the conditions were above chance. With regular feedback this was the case for symmetry/anti-phase trials, t(15)=2.3, p=0.034, while the other conditions were below chance. With transformed feedback all conditions were at chance level (symmetry/in-phase, t(15)=1.1; symmetry/anti-phase, t(15)=0.0; parallel/in-phase, t(15)=0.8; parallel/anti-phase, t(15)=-0.2).

Constant Error

There was a significant main effect for feedback, F(1,15)=129.2, p<0.001, showing that participants tended to be ahead for their ideal position with regular feedback, this positive bias disappears with transformed feedback.

4.3.4 Discussion

We wanted to investigate the impact of a rotation direction reversion between hand movement and the movement of the visual effect in a continuous circling task. With transformed feedback participants performance not only suffered like in previous experiments but became random in all conditions. This sheds new light on the importance of bodily feedback. Our previous results indicated that visual feedback is more important for our task than proprioceptive feedback. Although we always find reduced accuracy with a transformation present the same order in terms of difficulty for the conditions usually stays the same, e.g. participants perform more accurate in in-phase conditions. This does not seem to be possible for participants with this kind of transformation. The reason why this did not work in our case might be the nature of the used transformation. Mirror transformation seem to present a specially high demand and require extensive practice (Bedford, 1994). Our setup held the position on the y-axis constant between hand and visual feedback while the position on the x-axis changed. In a pointing/tracking study with asymmetries between x and y Beford hypothesize that transformations of that kind might not only be difficult to acquire but might even be learned incorrectly. Maybe if we had given participants extensive practice their performance would have improved. Shared movement direction in reference to the body was one of the influential factors we found in Experiments 1 to 4 . For Experiment 5 movement direction in reference to the body between hand and visual effect remained the same with the transformation present. However performance was at random with this transformation. This seems contradictory to our previous results. Maybe movement direction in reference to the body is just part of a greater spatial reference system that is used to match bodily movements to events in the environment. As we do find differences in the performance of symmetric and parallel rotations this might also be a part of the reference system. We found no in-phase benefit although phase of the movement is comparably unchanged, i.e. to produce in-phase movements the position on the vertical axis through the circle would be the same for stimulus hand and effect. Roerdink et al. (2005) report improved performance in anti-phase tracking with mirrored feedback. A closer look at their paradigm however reveals, that their setup rather matches the transformed conditions in Experiment 1 where the 180°phase shift turn an anti-phase cross-modal relation between hand and stimulus into an in-phase visual relation between feedback and stimulus. As their osscilatory stimulus movement had only one dimension (left - right) mirrored feedback equals 180°phase shifted feedback, whereas our two dimensional circling paradigm (left - right; up - down) differentiates between those two kinds of transformations. A way of improving performance might be to tell participants about the nature of the transformation. We tested this in a control experiment.

4.3.5 Control Experiment

We wanted to know whether knowledge of the nature of the transformation would improve participants performance in this task. We changed the instruction participants saw in the screen to specify the hand movement the was needed to produce the instructed effects.

Method

Participants Sixteen participants (four male and twelve female, aged 19 to 29 years, mean 22.9 years, SD 2.3 years) were paid to participate in a single session.

Procedure and design Experiment 6 differed from experiment 5 insofar as the nature of the transformation was explained to the participants in the instruction. The instruction participants saw on the screen prior to each trial was extended to specify the hand movement that was necessary to produce the requested effect. It now read e.g. parallel - produced by symmetric hand movement. We also changed our questioning of the participants after the experiment. While the questioning was rather open and unspecific before, we now asked them whether they payed more attention to their hand movement or to the effect on the screen and how they thought they managed the transformation. In addition to their verbal report, participants were asked to sketch their strategies for every condition in a schematic depiction of the display.

Results

The means and standard deviations (averaged across speed levels) for the different dependent variables are given in Table 4.5.

	Regular feedback				Transformed feedback			
	Symmetric		Parallel		Symmetric		Parallel	
	In-Phase	Anti-Phase	In-Phase	Anti-Phase	In-Phase	Anti-Phase	In-Phase	Anti-Phase
	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)
Instructed Mode %	66 (18)	11 (7)	64 (21)	43 (15)	26 (12)	27 (12)	27 (13)	26 (11)
Contrary Mode %	3 (5)	39 (14)	3 (4)	10 (8)	27 (11)	27 (11)	26 (11)	27 (14)
Constant Error	23 (11)	-28 (30)	28 (13)	20 (22)	0 (13)	0 (12)	1 (13)	-8 (22)

*Table 4.5: Note. All values for IM and CM differed significantly from the expected value for random performance (25%), * those values cannot be interpreted in a straightforward way because participants' performance was not predominantly in the instructed mode.*

Instructed Mode (IM) Figure 4.4 illustates the results for measure IM. There was a significant interaction Feedback x Direction x Phase, $F(1,14)=25.9$, showing that performance was at chance level with transformed feedback. With regular feedback, performance in symmetric/anti-phase conditions was below chance level, $t(14)=-7.3$,$p<0.001$, for the other three conditions performance was above chance , there was no difference in accuracy between the in-phase conditions, $t(14)=0.5$.

Contrary Mode There was a significant main effect for feedback, $F(1,14)=91.8$, showing that the time participants spent in CM was blow chance for regular feedback, $t(14)=-11.4$, $p< 0.001$, and at chance level with transformed feedback, $t(14)=1.8$. There was a significant interaction Feedback x Direction x Phase, $F(1,14)=18.5$, $p = 0.001$, showing that performance was at chance level with transformed feedback. With regular feedback there was no difference between symmetric/in-phase and parallel/in-phase conditions, $t(14)=0.2$, only for symmetric/anti-phase conditions performance was above chance level, $t(14)=3.9$, $p=0.002$.

Constant Error There was a significant main effect of feedback, $F(1,14)=55.2$, $p<0.001$, showing that participants were ahead of their ideal position with regular feedback, but this lead disappears with transformed feedback.

Questionnaire Participants reported to concentrate primarily on the visual effect presented on the screen especially with a transformation present. Only two of sixteen participants reported that they found the transformation hard to manage. In contrast to their verbal report that they concentrated on the visual effect in the transformed conditions about seven of the participants depicted stimulus-movement constellations in the drawings of of their coordination strategies instead of stimulus-feedback constellations.

Discussion

Knowledge of the nature of the transformation did not influence performance. Maybe participants can not consciously influence the processes that are responsible for the destruction of performance with transformed feedback. Our results point to the importance of crosstalk between motor and visual characteristics of an action. In previous experiments we found evidence for visual dominance meaning that visual features of movement effects are important for their coordination with external events. However we always found costs if movement and effect are somehow dissociated. In the current experiments those cost are so high that coordination is actually impossible. It is assumed that the reasons for the participants' failure are to be found on a cognitive rather than on the motor level, as the transformation does not change the motor demands of the task. This is in accordance with results of a study by (Sutter, 2007) who studied motor learning using laptop input devices that employed different transformations. The author concludes that rather cognitive representation of transformation hinders learning than pure motor aspects. If the current transformation is not correctly represented, fast adaption is hindered.

The fact that participants have so many problems with this mirror transformation counteracts another finding of our previous studies. As mentioned before we always found an in-phase benefit, i.e. participants showed better results if they were instructed to produce in-phase movement patterns compared to anti-phase movement patterns. Moving in-phase involves that visual effect and stimulus maintain the same position on the y-axis, whereas the position on the x-axis could be different, depending on the instructed movement direction. What we found was that the same position on the y-axis helped participants to coordinate with the stimulus, whereas it made no difference if the position on the x-axis was the same or different. In other words, if movement direction in reference to the body was the same between stimulus and feedback this usually improved performance. From those results one should expect that participants should be able to handle the mirror transformation because here as well the position on the y-axis stayed the same while the position on the x-axis was manipulated.

An alternative strategy to deal with this transformation could have been to ignore the confusing visual feedback and solve the task by concentrating on the hand movement exclusively at least in the control experiment. Obviously participants did not chose this, either because visual feedback is so salient that it can not be suppressed and ignored, or because participants were instructed on the visual feedback. This strategy would also require participants to be aware of their failure in the first place and look for alternative strategies to solve this task. As our questionnaire showed participants lacked this insight.

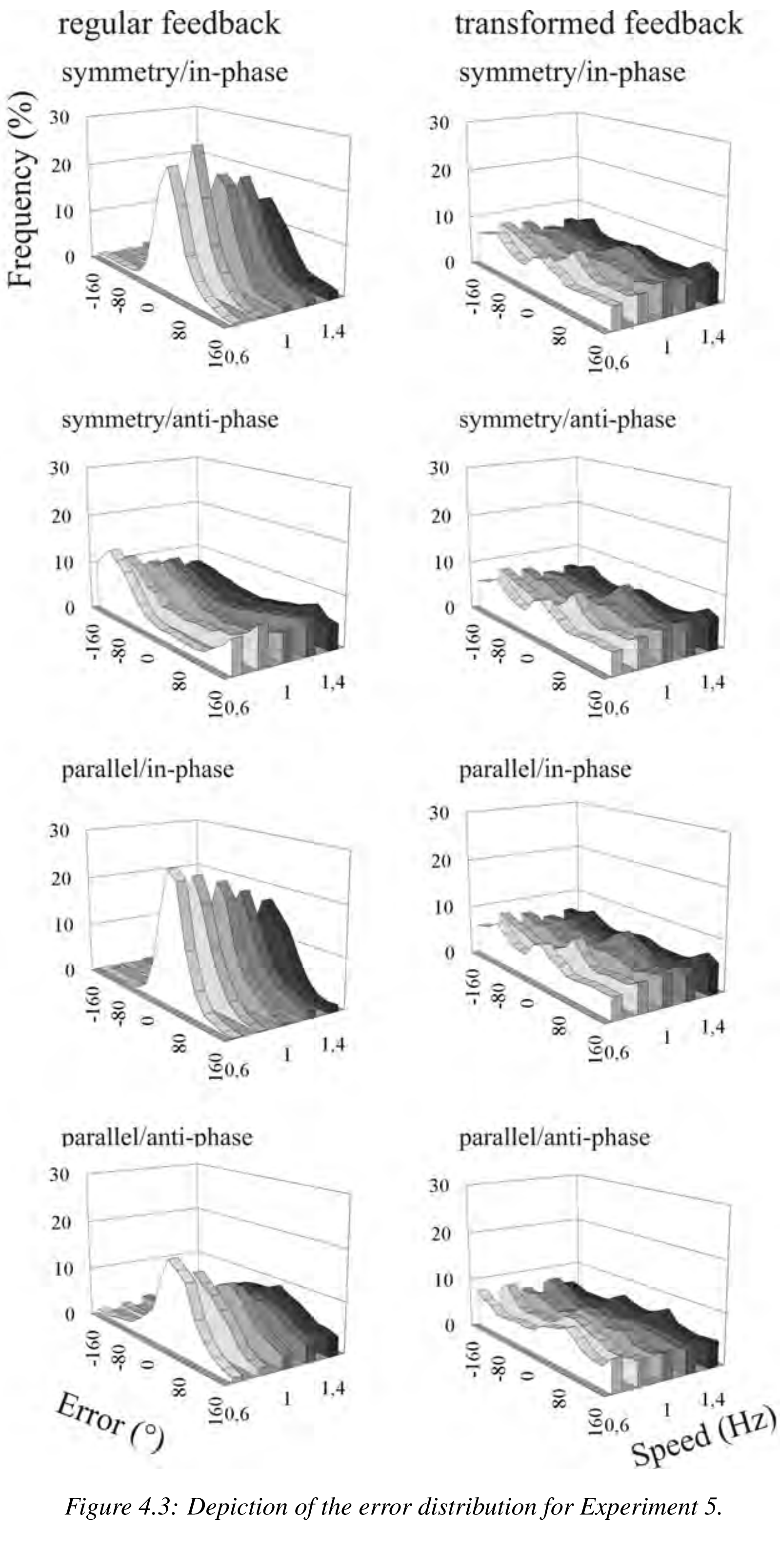

Figure 4.3: Depiction of the error distribution for Experiment 5.

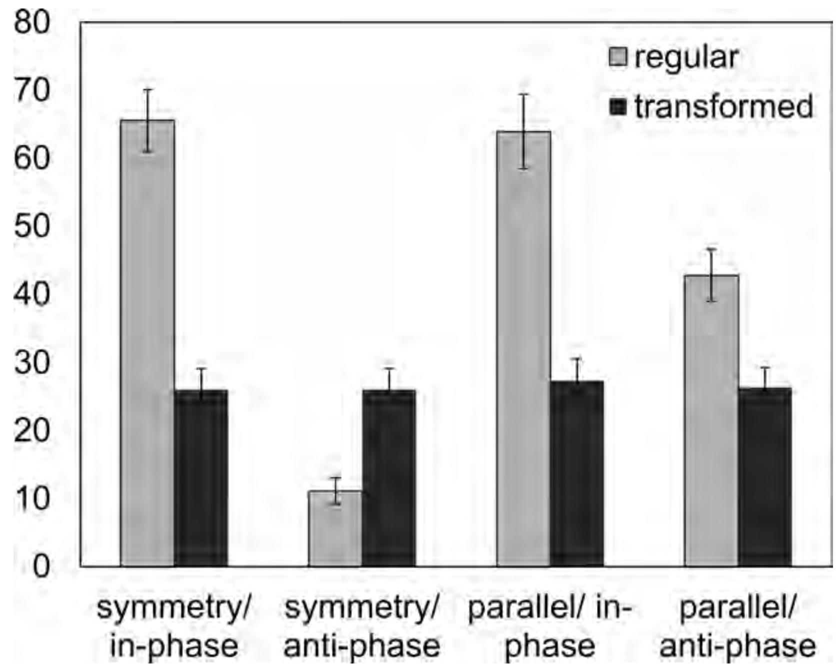

Figure 4.4: Depiction of results for measure IM for Control Experiment to Experiment 5.

4.4 Experiment 6 - Gain

4.4.1 Introduction

In previous experiments we found that accuracy of coordination decreased with higher speed levels. The question arises whether this reflects increased motor demands because of the faster movements or if it is due to higher perceptual demands because there is less time to process visual input, to predict the correct next position and transmit adequate commands to the motor system. In our previous experiments motor speed and visual speed always were the same.

Most of the previous studies have investigated the influence of different gains in straight movements. In this experiment we are going to investigate how the perceptual-motor system deals with transformations scaling gain in circling movements. Circling movements differ from straight movements when a gain unequal to 1 is introduced between action and effect. In straight movements with a gain unequal to 1 different distances are covered by the hand and the visual effect but still motor and visual reversal point coincide. A gain unequal to 1 in circle drawing results in a constant change of the mapping of positions on the movement trajectory to positions on the visual trajectory. For example, in one circle, participants may be on the right side of the movement circle but on the left side of the effect circle. A couple of circles later both movement and effect could be on the same side. It was previously shown that in bimanual circling highly complex movements, even "impossible" movements (i.e. left and right hand circling in a 4:3 frequency ratio) can be performed when the visual feedback is simple (Mechsner et al., 2001, i.e. two circles moving in symmetry). However, that those movements can be performed does not necessarily mean that performance does not suffer from the presence of a transformation in comparison to a condition in which no transformation is present.

We used a unimanual circling task. An effect dot (produced by the participants' movement) had to be coordinated with a continuously circling stimulus dot, in order to produce mirror symmetric movements of the two dots on the screen. The movement angle of the hand was multiplied by a gain factor before being presented on the screen. This allowed us not only to compare transformed vs. regular trials (Roerdink et al., 2005; Mechsner et al., 2001, e.g.) but also to vary the magnitude of the transformation (we used 4 gains smaller than 1, a gain of 1, and 4 gains larger than 1) and to study the impact of transformation magnitude on coordination performance. We further varied the speed of the effect dot in 3 levels, because previous studies have shown that coordination performance deteriorates when movement and/or effect speed increases (Byblow et al., 1995; Heuer, 1993; Roerdink et al., 2005), especially under transformation conditions (Alaerts et al., 2007; Salter et al., 2004, e.g.).

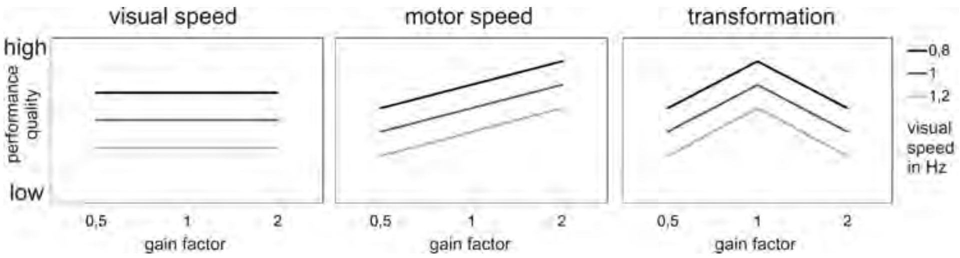

Figure 4.5: Depictions of the possible outcomes of this experiment. If visual speed is dominant increasing gain should make no difference for performance quality. If motor speed prevails performance quality should increase with gain. If the size of the transformation is the strongest predictor for performance performance quality should be best at gain 1 and decline with distance to 1.

We expected to find deterioration in performance with increasing visual speed (the 3 speed levels in our task). If a simple visual pattern is all that matters for coordination, the different gains between hand movement and effect movement should have no effect on performance, i.e. the quality of performance should be equal for different gains. If motor speed is important for coordination performance, performance should decline with smaller the gains, because smaller gains imply more distance has to be covered in the hand movement to produce a certain effect on the screen. Therefore the movements have to be faster. However, if it matters that a transformation is introduced between movement and effect, the best performance should be observed at a gain of 1 and performance should be worse at both, gains smaller and gains larger than 1. If performance is worse in conditions with a gain unequal to 1, we were further interested to see whether the magnitude of the transformation matters for performance. On the one hand, one could expect that all gains which do not equal 1 are performed equally well (or bad), because they all imply a constant change in the mapping of hand position to effect position. On the other hand, the mapping change is more drastic in gains which show a larger deviation from 1 than in gains that show a smaller deviation. Thus, performance may vary

gradually.
We know from experiments 1-3 that participants show systematic changes in their constant error depending on task and task difficulty. Participants usually show a positive bias which is however reduced with higher movement speeds. Thus, in our experiment the constant error could be interpreted as an indicator of task difficulty. Additionally, we were interested in whether participants would show visual anchoring i.e. reduced variability at salient locations on the trajectories. With the instruction we are going to use it has been previously shown that anchoring predominantly occurs in the north location of the stimulus circle. In Experiment 1 this effect was also found under transformation conditions, however the transformations did not consist of any gain changes, but a constant shift of the effect relative to the hand (e.g. 180°). The mapping of movement positions to effect positions was therefore constant in those experiments. We were wondering whether visual anchoring still occurs at location North when the mapping of movement positions to effect positions constantly changes.

4.4.2 Method

Participants

Sixteen adults (nine female and seven male, aged 20 to 28 years, mean = 24.4 years, SD = 2.25 years) participated in a single session.

Procedure and Design

Participants were instructed to produce mirror symmetric movements of the dots on the screen. They were asked to move their hand in counter-clockwise direction and they had to match the speed of the effect dot to the speed of the stimulus dot. We chose to use only this one condition in order to keep the experiment at a reasonable length. The relation of the speed of the hand movement and the speed of the effect dot was manipulated by introducing different gain values. The angle the hand moved between two sequentially measured points was multiplied by a gain factor between 0.5 and 2 before being displayed on the screen. There were nine different gains, four smaller than 1 (0.5, 0.6, 0.75, 0.8), requiring the hand movement to be faster than the movement of the effect dot (MoFast trials), four larger than 1 (1.25, 1.3, 1.5, 2), requiring the hand movement to be slower than the movement of the effect dot (MoSlow trials), and 1. The rationale for choosing those gain factors was to use the non harmonic patterns Mechsner et al. (2001) mentions which are 5:4 (1.25) and 4:3 (1.3). We also used the reciprocals of those ratios, because it might not make such a big difference if the right hand is doing 5 turns while the left hand does 4 turns or vice versa[1], but it might make a big difference whether the feedback is speeded up in relation to the hand or if it is slowed down. Thus we used 4:5 (0.8) and 3:4 (0.75) and than amplified the range of the ratio to 1:2 (0.5) and 2:1 (2) choosing 2:3 (0.6) and 3:2 (1.3) as intermediate steps. Each gain was presented in one block of eight trials. The order of the blocks (and therefore the gains) was randomized between participants. Participants had to go through 9 blocks. After 5 blocks there was a 3 minute break.

After reading the instruction participants saw a demonstration of the mirror symmetric movements they were to produce. Every 10 circles it increased its speed by 0.2 Hz, starting at 0.8 Hz and finishing at 1.2 Hz. Each trial lasted 31 s, effective testing time was 37.2 minutes, however, due to breaks between the trials participants needed about an hour to complete a session. After the sixth trial in each block participants were asked to rate whether a transformation was present in the last trial. A 5 step scale (1 = certainly not present; 2 = likely not present; 3 = undecided; 4 = likely present; 5 = certainly present) was presented on the screen. Participants' decision was recorded by the experimenter.

4.4.3 Results

The distribution of CE values can be seen in Figure 4.6.

Instructed Mode (IM)

The results for IM are depicted in the upper part of Figure 4.7 and show a decline in performance with increasing distance of of gain from 1. A repeated measures ANOVA with the factors Gain (0.5, 0.6, 0.75, 0.8, 1, 1.25, 1.3, 1.5, 2) x Visual Speed (0.8 Hz, 1 Hz, 1.2 Hz) was conducted on IM. There was significant main effect of Visual Speed, $F(2,30) = 26.7$, $p < 0.001$, showing that accuracy declined with increasing speed. There was also a significant main effect of Gain, $F(8,102) =$

[1]Mechsner et al. (2001) only report to have used a 4:3 ratio to the right crank.

10.8, $p < 0.001$, showing that the best performance was observed with gain 1, i.e. the regular action-effect relation. Performance suffered with gains larger or smaller than 1. Within the MoSlow trials the magnitude of the gain factor did not matter, there was no difference in performance for the four steps. For the MoFast trials however, we found that performance declines in two steps, first from gain 1 to gain 0.8 with no difference in performance between 0.8 and 0.75 and in a second step to gain 0.6 with no difference in performance between 0.6 and 0.5. A significant interaction Gain x Visual Speed, $F(16, 240)=3.9$, $p<0.001$, modified those effects. It reflects that performance differences due to different levels of visual speed were smaller in MoSlow (maximal difference = 7.05 %) than MoFast trials (maximal difference = 18.9 %).

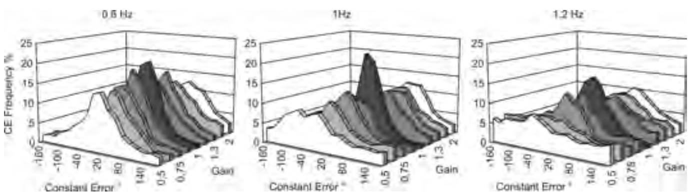

Figure 4.6: Frequency distributions (in %) of Constant Error values for the 9 gain levels, separately for the 3 different levels of visual speed

Constant Error (CE)

The results for CE are depicted in the middle part of Figure 4.7 and show that CE increases with Gain. A repeated measures ANOVA with the factors Gain (0.5, 0.6, 0.75, 0.8, 1, 1.25, 1.3, 1.5, 2) x Visual Speed (0.8 Hz, 1 Hz, 1.2 Hz) was conducted on CE. There was a significant main effect of Visual Speed, $F(2,30)=43$, $p< 0.001$, showing that participants were more likely to lag behind the stimulus with higher speed than with lower speed. There was also a significant main effect for Gain, $F(8,120)=18.2$, $p < 0.001$, CE values are negative for small gains an increase with larger gains. There also was a significant interaction Gain x Visual Speed, $F(16,240)=1.9$, $p < 0.018$, showing that whereas in MoFast trials CE was similar in the 1.0 and 1.2 Hz visual speed conditions and was more positive in the 0.8 Hz condition, in MoSlow trials CE was similar for the 0.8 and 1.0 Hz condition, and was less positive in the 1.2 Hz condition.

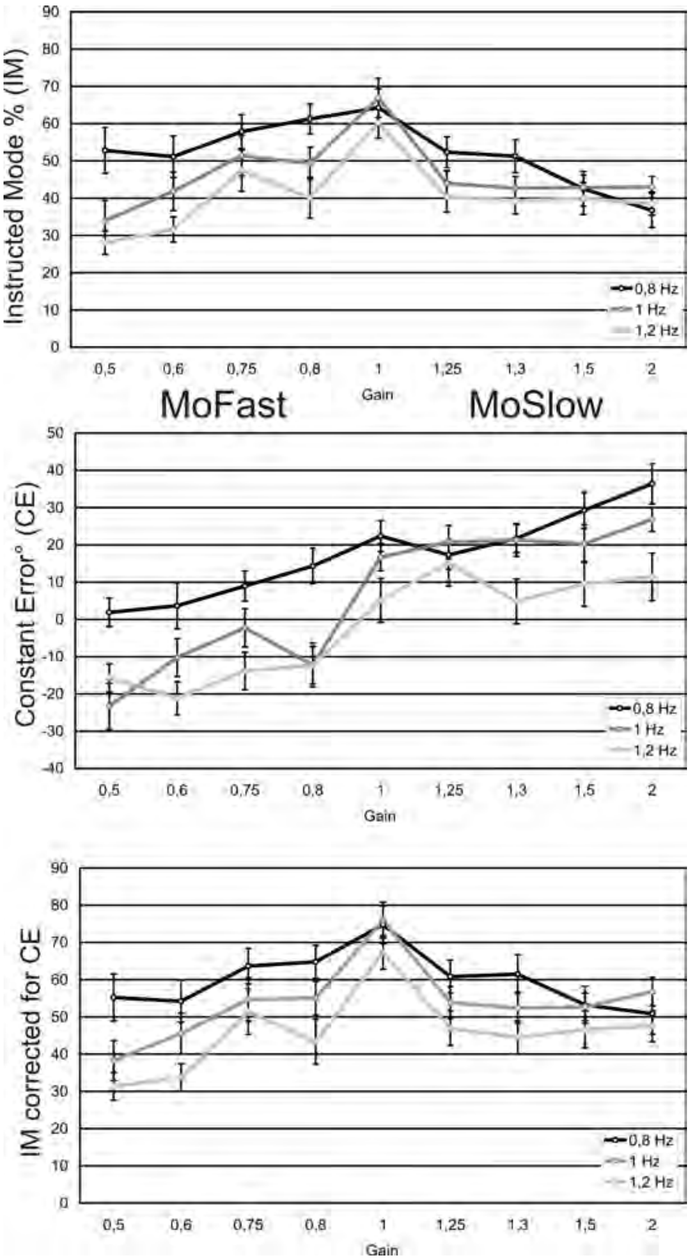

Figure 4.7: Graphical depiction of means and standard errors for the variables Instructed Mode, Constant Error and Instructed Mode corrected for Constant Errors depending on 3 levels of visual speed and 9 levels of gain. Note that for all gain levels < 1, speed of the movement is higher than speed of the feedback (MoFast) while for gains > 1 movement speed is slower than feedback speed (MoSlow). All values for IM are significantly different for expected value with random performance which is 25%.

Control Analyses: IM calculated from the Mean CE

One may argue that variations in IM are mainly due to the fact CE is negative in MoFast trials and positive in MoSlow trials. Because IM was calculated by using CE values within +/- 45 degrees around 0, it may be that when the mean CE deviates from 0 parts of the distribution around it are systematically not used in the calculation of IM. Though some aspects of our data speak against this interpretation (e.g. with gain 1 CE values are already positive), we still wanted to rule out this possibility statistically. We calculated the IM again, using the participants mean CE +/- 45°for each conditions. The results for IM corrected for mean CE values are depicted in the lower part of Figure 2. The data were analyzed in a repeated measures ANOVA with the factors Gain (0.5, 0.6, 0.75, 0.8, 1, 1.25, 1.3, 1.5, 2) and Visual Speed (0.8 Hz, 1 Hz, 1.2 Hz) The results were similar to the original analysis of IM. We found significant main effects for Gain, $F(8,120)=12.4$, $p<0.001$, and Speed, $F(2,30)=41$, $p<0.001$, showing that best performance was observed with gain 1 and accuracy that decreased with increasing speed. Again there was no difference in performance as a function of magnitude of gain in MoSlow trials, and in MoFast trials performance declined in two plateaus, from 0.8 to 0.75 and 0.6 to 0.5. A significant interaction Gain x Speed, $F(16,240)=2.1$, $p=0.009$, showed that differences between the speed levels were smaller for MoSlow trials than for MoFast trials. Thus, negative and positive CE values did not obscure the general data pattern of IM.

Variable Error (VE)

Results for VE are depicted in Figure 4.8. A repeated measures ANOVA with the factors Gain (0.5, 0.6, 0.75, 0.8, 1, 1.25, 1.3, 1.5, 2) , Visual Speed (0.8 Hz, 1 Hz, 1.2 Hz), and Location (24 sections of 15°each) was conducted on VE. There was a significant main effect for Location, $F(23,345)=15$, $p<0.001$, showing that variability of the effect dot was lowest between 270° and 360°, i.e. between locations north and east. There also was a significant main effect for Visual Speed, $F(2,30)=53.7$, $p<0.001$, showing less variability at slower speed levels than at faster speed levels. The differences between locations were more pronounced for slower visual speed than for faster visual speed, as indicated by the interaction Visual Speed x Location, $F(46,690)=1.6$, $p=0.009$. There was a significant main effect of Gain, F(8,120)=13.2, p<0.001, showing less variability in the gain = 1 condition than in the other gain conditions, and a significant interaction Gain x Location, F(184,2760)=1.6, p<0.001, reflecting that the difference between locations was smaller for gain =1 compared to the other gain factors. An interaction of Gain x Speed, F(16, 240)=2.6, p=0.001, showed that differences between the speed levels were smaller for MoSlow trials.

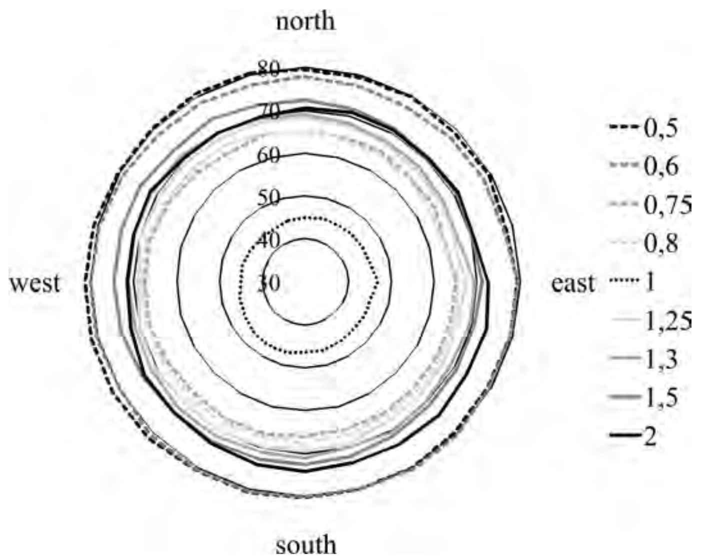

Figure 4.8: Graphical depiction of means and standard errors for the variable Variable Error depending on 9 gains and 24 locations, separately for the 3 different levels of visual speed.

Gain	0.5	0.6	0.75	0.8	1	1.25	1.3	1.5	2
Mean (SD)	4.4 (1.3)	4.5 (1.1)	3.4 (1.7)	3.6 (1.2)	2.3 (1.2)	3.3 (1.4)	2.5 (1.3)	4.1 (1.0)	4.0 (1.4)

Table 4.6: Note: Verbal encoding for the ratings: 1= certainly not present, 2= likely not present, 3=undecided, 4=likely present, 5=certainly present.

Questionnaire

The mean ratings and standard deviations are displayed in Table 4.6. An ANOVA with the factor Gain (0.5, 0.6, 0.75, 0.8, 1, 1.25, 1.3, 1.5, 2,) on mean rating was significant, F(8,112)=9.9, p < 0.01. In the gain = 1 condition the presence of a transformation was least likely to be reported. Participants were more likely to report the presence of a transformation the larger the gain deviated from 1.

4.4.4 Discussion

In the presented experiment we investigated how the perceptual-motor system deals with action-effect transformations in unimanual circling. Participants had to coordinate the visual effect of their hand movement with a continuously circling stimulus in order to produce mirror symmetric movements of two dots on the screen. The movement angle of the hand was multiplied by a gain factor before being presented on the screen. We used 4 gains smaller than 1 (MoFast), a gain of 1, and 4 gains larger than 1 (MoSlow). We further varied the speed of the effect dot in 3 levels. Performance was best in the gain = 1 condition. In the MoFast condition, performance successively deteriorated, whereas this was not the case in the MoSlow conditions. Performance differences due to different levels of visual speed tended to be smaller at MoSlow than MoFast trials. Participants were more likely to lag behind the stimulus with higher speed than with lower speed. Further, with small gains participants lagged behind the stimulus, whereas with higher gains participants were in advance of the stimulus. Participants showed anchoring at location north.

Our main finding is that the mere presence of a transformation negatively affects coordination in unimanual circling. Performance with regular feedback (gain = 1) was more accurate than performance with gain larger or smaller than 1. This shows that the visual pattern produced by a movement is not sufficient to explain coordination performance, because if that were the case the different gains between hand movement and effect movement should have no effect on performance. Difficulty of the task did also not simply depend on motor speed, because then a decline from large to small gains should have been observed. Rather, the results are in favour of the assumption that the presence of a transformation itself affects performance which is in accordance with results showing that the transformation is an important part of the cognitive representation of tool-use actions (Massen & Prinz, 2007; Lepper et al., 2008). The results are in contrast to studies in which straight movements were investigated: here accuracy steadily decreases with increasing gain (Rieger et al., 2005; Rosenbaum & Gregory, 2002). This difference between straight and circling movements may be because circling movements imply a constant change in the mapping of hand position to effect position in the presence of a gain, which is not the case in straight movements.

We were further interested to see whether the magnitude of the transformation or merely its presence matters for performance. The data are contradictory here: on the one hand in MoSlow trials performance did not differ between different gains, whereas in MoFast trials it did. This effect of transformation magnitude in the MoFast trials may be due to motor speed: coordination may be more difficult with faster speed due to higher demands on the motor system. This is in accordance with the observation that performance differs due to different levels of visual speed (which also implies faster motor speed) tended to be larger in MoFast than MoSlow trials. With larger gains, movements were slower (MoSlow). Here it seems that the magnitude of the gain does not matter but only the presence or absence of a transformation. Because motor demands are generally lower in the MoSlow trials it could be that differences in gain (and correspondingly in motor speed) no longer influence performance. Thus, when motor demands are low, different gain magnitudes are performed equally well (or bad), because they all imply a constant change in the mapping of hand position to effect position, regardless of how drastically the mapping changes from circle to circle. The reason for the stepwise decline of performance in the MoFast trials might be due to our choice of gain steps. As discussed in point 4.4.2 those gain steps are theoretically motivated and are therefore not equidistant. If we choose gainsteps of regular distances we might have found a steady decline of performance in the MoFast trials.

The way the task was performed was systematically influenced by the magnitude of the transformation and by visual speed. Participants were behind their ideal position in MoFast trials and came closer to the ideal position with increasing gain. With gain = 1 and in MoSlow trials participants were ahead of their ideal position. It seems that the data pattern of the Constant Error is related to movement speed and not to effect speed. If effect speed were the decisive factor, the different gains applied should not have made a difference. The gain alone can also not explain the observed pattern of results, because visual speed (and correspondingly movement speed) had a systematic effect. It is however possible that gain has an effect in addition to the effect of movement speed. It seems plausible that under conditions in which movements are slow and coordination is relatively easy the default coordination mode entails that the effect dot is ahead of the stimulus. We think that participants use some kind of predictive mechanisms (predicting the stimulus position, effect position, or both) to accomplish the task. In conditions without transformations this results in the effect being ahead of its ideal position. The reason for this may be a mechanism similar to the one responsible for the negative asynchrony in tapping (Aschersleben & Prinz, 1995, e.g.). In tapping, the tap of the finger precedes the tone with which synchronization has to occur. If there is a transformation present this has to be taken into account to make appropriate predictions. Our data suggest that this may be insufficiently accomplished: with high gains the effect resulting from a movement might be underestimated, resulting in the effect being in advance of the transformation. Conversely, with small gains, the effect produced by the movement may be underestimated, resulting in the effect lagging behind the stimulus.

As we expected for our chosen visual setup participants used location north for anchoring. The fact that anchoring is more pronounced for gains different from 1 reflects the increased task demand by the presence of a transformation. Stronger use of salient visual task characteristics might be a way to meet those demands.

The magnitude of gain had an impact on participants' conscious experience of the transformation. The greater the gain diverged from gain 1, the more likely participants noticed the presence of a transformation. This was the case in MoFast as well as MoSlow trials. This effect was interesting: one could have expected that due to the constant change of the mapping of movement positions to effect position with any gain other than 1 a transformation would always be detected. Further, even with small gain deviations from 1 there are eventually circles in which movement and effect are on opposite sides. This indicates that awareness of the actual position of the hand may have been limited and that the magnitude of the transformation may be more important for detecting it than a mismatch between movement and effect position. This is in accordance with other studies indicating that participants are not very good in knowing their actual hand positions in similar tasks and that the magnitude of a perturbation plays an important role for detecting it (Fourneret & Jeannerod, 1998; Koblich & Kircher, 2004).

Temporal variability increases with cycle duration(Killeen & Weiss, 1987; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). Whether this is due to motor or visual processes we cannot answer with our paradigm. Our results suggest a mutual dependence between the two.

Gain	0.5	0.6	0.75	0.8	1	1.25	1.3	1.5
	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)
IM %	38 (17)	42 (17)	52 (18)	50 (16)	64 (17)	46 (13)	44 (13)	42 (14)
CM %	15 (8)	16 (8)	9 (8)	10 (8)	4 (5)	9 (7)	10 (6)	12 (10)
CE	-12 (12)	-9 (12)	-2 (15)	-3 (14)	15 (13)	18 (15)	16 (14)	20 (18)

Table 4.7: Means and standard deviations for measures IM, CM and CE for Experiment 6.

We conclude that the mere presence of a transformation has a negative impact on performance in situations in which the mapping of hand position and effect position is not constant due to its presence. The way movements are performed (whether produced effects follow the stimulus or precede it) may be due to flaws in the representation of the gain. Anchoring occurs at visually salient locations. Participants' conscious experience of the transformation depends on the deviation of the gain from 1. When designing machines or tools that involve transformations between movements and their external consequences, one should be aware that the mere presence of angular gains may result in performance decrements.

4.5 General Discussion Part II

In this second part of the dissertation, we presented three experiments which employed different transformations. In Experiment 4, we used phase shifts of different size both in the direction of the rotation (positive phase shifts) and against the direction of the rotation (negative phase shifts). Positive phase shifts evoked the feeling that the feedback was running ahead of the hand. This was less disturbing for performance then negative phase shifts, which evoked the feeling of the feedback trailing behind the hand. In Experiment 5, we used a transformation that mirrored the position of the hand at the vertical axis through the center of the trajectory, which resulted in a reversal of rotation between hand and feedback. This was by far the hardest transformation we confronted participants with, as they completely failed to manage the coordination task in this experiment. Finally, in Experiment 6, participants had to cope with differences in gain between hand and feedback. With gains smaller than 1, the hand moved faster than the feedback (MoFast trials) and with gains larger than 1 the feedback moved faster than the hand (MoSlow trials). With MoFast trials performance successively deteriorated, while with MoSlow trials performance was less accurate than with regular feedback but was not sensitive to increase in gain beyond that.

Common to all our experiments, performance quality decreased in transformed conditions compared to conditions with regular feedback. In general, the bigger the transformation magnitude, and with this, the discrepancy between the actual movement and its visual feedback, the bigger the impact on performance. Phase shifts seem to easier to process as the general level of performance was higher in Experiment 4 than in Experiment 6. This might be due to the fact that phase shifts still allow an unambiguous and persistent spatial mapping of the feedback position on the hand position. For example; with a phase shift of 180°, hand position south is always presented as feedback position north. This is not the case for transformations of gain, where the ration of the covered distance stays the same, e.g. for gain 0.75, the hand moves 100° while the feedback only moves 75°, but the spatial position of the feedback cannot be predicted only on the basis of the current position of the hand. Instead, the previous positions have to be taken into account to estimate the movement-feedback relation and predict the results of the next movement. This presents increased demands to the motor system, which are reflected in reduced movement efficiency.

Participants had to deal with so-called opaque transformations, i.e. they were not told what kind of transformations were applied to their hand movements. The only exception to this routine was the control experiment for Experiment 5, where we explicitly told participants what the relation between their hand movement and the visual feedback would be before every single trial. This had no effect on performance however.

Mirror transformations like those used in Experiment 5 seem to present a unsolvable problem, at least if participants are not allowed to practice in advance. Some characteristics of the task, like the unambiguous spatial mapping of feedback to hand position or the fact that movement direction in reference to the body is maintained, suggest a manageable task. Still, participants' performance was entirely random. Mirror transformations seem to go beyond our spontaneous sensory-motor abilities and need extensive practice in order to be accomplished (Bedford, 1994). The reason for this might be conflicting direction feedback between proprioception and vision in the azimuthal plane. While the hand moves to the left and reports this via afferent fibres to the CNS, the visual feedback moves to the right which is monitored by the CNS via the retina. As feedback from vision and proprioception is integrated into motor planning in order to enhance accuracy, the CNS has to ignore the afferent information from the limbs to some extend, which is very demanding. With deaffarented subjects this crosstalk does not exist and they are capable of mirror drawings without considerable practice (Guedon et al., 1998).

In order to achieve goal-oriented and effective motor behavior the CNS has to control movements, i.e. translate intended effects into motor commands and predict the consequences of those movements. The neural processes underlying control and prediction are referred to as inverse and forward models (Jordan, 1996; Wolpert & Ghahramani, 2000; Wolpert & Flanagan, 2001). Both models are tightly coupled and are constantly updated through experience. There is evidence that prediction is learned faster than control (Flanagan, Vetter, Johansson, & Wolpert, 2003), i.e. when confronted with a new object, we are faster in learning to predict the object than learning to control the object. Applied to our paradigm, this would mean that when the transformation is integrated into motor planning, participants are able to predict the consequences of executed motor commands while the transformation is active, but control is not yet accomplished. Experimental evidence for this model is the positive bias in the Constant Error values, which we interpret as a result of predictive motor planning, while reduced performance accuracy in the coordination task shows that control is not yet achieved. This effect might be amplified by the lack of extensive training before the task. Participants had only three training trials to get used to the task. A way to check the validity of these assumptions would be to give participants extensive training and measure how adaption to the transformation develops with the amount of training. For some transformations it might be possible that participants come close to performance with regular feedback, as has been shown for the use of a computer mouse (Brenner & Smeets, 2003).

To conclude, the nature and magnitude of a transformation determine how much the transformation will affect performance. Transformations employing stable spatial mappings between hand position and feedback position are easier to accomplish than those with flexible mappings. Mirror transformation are not manageable without extensive practice, even if the transformation rule is revealed to the participants.

Chapter 5

General Discussion

This dissertation introduces a versatile paradigm, which was established in bimanual research (Mechsner et al., 2001; Tomatsu & Ohtsuki, 2005) and was adapted for unimanual coordination research. The paradigm allowed us to manipulate visual arrangements, the relation between hand movement and visual feedback, and also movement speed. The experiments we conducted using this paradigm investigated the role of effect vs effector in the coordination of unimanual continuous movements. The motivating question was in what way the characteristics of the movement effects and the relations between these effects and the actual movement affect performance.

5.1 Summary of Experimental Findings

Our movements are influenced by the ever-changing environment and our body. In this study, we used a circling paradigm to identify and study characteristics of motor coordination in unimanual continuous tasks. We manipulated visual feedback in two ways, once by changing the spatial relationship of stimulus and feedback dot by presenting them e.g. horizontally (Experiment1) or vertically aligned (Experiment 3) and on interleaved trajectories (Experiment 2). Second, we gave participants different instructions on the movement patterns they were to produce in the spatial setups, e.g. symmetry/in-phase, symmetry/anti-phase, parallel/in-phase, parallel/anti-phase. Both manipulations resulted in differences in performance quality and affected anchoring, i.e. the strategic use of visual information for motor coordination.

Participants employed a predictive strategy to plan their movements and used information about movement direction in reference to the body, or rather changes in that direction, to structure their circular movements. By employing transformations, we deliberately created correspondences in properties of movement and stimulus or feedback and stimulus. Performance benefited from correspondences between feedback and stimulus, supporting our hypothesis that unimanual coordination with external events functions as effect-stimulus-coordination. By applying a wider range of transformations (Experiments 4 to 6) we showed that the way a transformation affects performance depends both on its physical characteristics, like nature (e.g. phase shift, angular gain or direction reversal) and magnitude, and the subjective qualities perceived by the participants.

In a first set of experiments, we manipulated the visual context of the movement effect but kept the relation between movement and effect constant and rather simple. We found evidence that unimanual continuous movement coordination functions as effect-to-stimulus coordination rather than movement-to-stimulus coordination. Our results show that the visual setup influences coordination performance significantly. By changing the perceptual input, the accuracy of performance could be increased, e.g. by placing stimulus and effect close to each other, or decreased, e.g. by separating them further. It also became clear that certain phenomena known from bimanual studies with similar paradigms cannot be transfered to unimanual coordination. For instance, the benefit for mirror symmetric movement patterns does not occur in unimanual coordination.

In the second part of the dissertation, we manipulated the relation between the actual hand movement and the effect using phase shifts, direction reversals or amount of angular gain.

Transformations are incorporated into movement planning but are not consciously available to the actor. Visual feedback is crucial for coordination and cannot be ignored even if the complex movement-feedback-relation hinders coordination (Experiment 5). We find that small phase shifts are integrated into motor planning very well, but performance declines as a function of phase shift magnitude, with lowest accuracy at 180°. The same is true for gain, where it also makes a difference whether gain is positive or negative even when the amount of alteration is the same. Mirror transformations however, like the one we used in Experiment 5, disrupt performance completely. They seem to go beyond what our sensory-motor system can accomplish and might not be integrated correctly even after extensive training (Bedford, 1994).

We cannot make reliable assumptions on how participants experienced our task and how consciously they processed the transformation. Our questionnaires only provides a superficial impression on what participants thought and felt. There are several reasons for this. In the first experiments, we tried to direct as little attention as possible to the presence and nature of the transformation. This was because we did not want participants to think about the transformation or use any conscious strategies. We mentioned the presence of a transformation in the instruction but did not make any further remarks or explanations. After the experiments we asked open questions “How did you deal with the transformation?” with the hope of getting a more individual impression of what participants felt. The only experiment where we explicitly explained the nature of the transformation was the control experiment in Experiment 5, where we also reminded the participants of the movement-feedback-relation by spelling it out before every single trial. However, this did not change our results. The explicit knowledge of the results did not help participants in dealing with the transformation nor did it improve their awareness of their poor performance.

However, participants were able judge the presence of a transformation when asked during the experiment like in Experiment 6.

From our results, one would induce that the way the motor system incorporates visual-motor-transformation is not consciously accessible. This means knowing or explaining the transformation has little effect on the way this transformation is dealt with. The motor system has to be trained to accomplish this task and theoretical knowledge does not improve it (Sutter, 2007). It might be that even with extensive training performance will never be perfect (Albert & Ivry, 2009).

5.2 Theoretical Implications

5.2.1 Vision-to-Stimulus Coordination

Our results support the conclusion that motor coordination is predominately vision-to-stimulus coordination. We showed that “easy” visual in-phase relation was preferred to cross-modal in-phase relation in conditions where actual movement and visual effect were dissociated by a visuomotor transformation. This was true for all experiments, except experiment 5 where the disruptive effect of the transformation prevented any coordination. The quality of the vision-to-stimulus coordination was modulated by the transformation and the visual setup.

Our conclusion that coordination in our paradigm is vision-to-stimulus coordination is in accordance with the ideomotor principle, which states that actions are represented in terms of their perceptual consequences (James, 1890; Hommel, Müsseler, Aschersleben, & Prinz, 2001). As our participants were instructed on the visual effects of their actions, this is what they anticipate, and movements are selected and initiated to achieve these effects. Another fact that proves the importance of the effect of the movement is the finding that changes in the visual setup were reflected in changes in coordination performance. This can only be due to the visual effects of the action because motor demands stayed the same. Performance quality depended on difficulty of the visual setup. A simpler visual setup in terms of a good homogeneous Gestalt resulted in better coordination performance. If movement characteristics were the primary determinant of coordination, the different visual setups should not have made a difference, as the motor demand of turning the crank stayed the same between the experiments.

5.2.2 Movement-to-Stimulus Coordination

With transformed feedback, the action-perception relationship gets more complex. We still find that coordination takes place between the stimulus and the visual effect of the movement. However, performance is impaired by the dissociation between actual movement and visual feedback on the screen. This impairment is modulated by the nature and magnitude of the transformation.

It seems to be crucial that the effects can still be ascribed to the actual movement (Wulf & Prinz, 2001), i.e. if movement and feedback are separated too far, performance is random. This was the case with the mirror transformation in Experiment 5. We assume that the problems with the mirror transformation are due to crosstalk and controversial direction information between proprioception and vision. As both channels of information are integrated into motor planning, it takes extensive training to enable the CNS to make sense of this contradictory information.

5.2.3 Anchoring

Anchoring was very flexible and could be movement- or vision-related. Participants used locations that were perceptually salient for both the current visual setup in general and for the specific conditions. The more the conditions differed in their perceptual features or possible cognitive workload, the more likely it was that anchoring locations also differed. Anchoring was an effective strategy to structure more demanding visual movement patterns. The differences in anchoring between in-phase and anti-phase conditions might be explained by different eye movements in these conditions. Huys, Williams, and Beek (2005) studied gaze behavior in perception and production of in-phase and anti-phase patterns in a unimanual tracking task. The authors report different modes of gaze control for the two tracking modes. With in-phase tracking, participants predominantly used smooth pursuit visual tracking while for anti-phase tracking visual tracking was replaced by saccades and episodes of gaze fixation. Unfortunately, we did not record the eye movements of our participants (see 7.4. for further discussion). With respect to anchoring Roerdink et al. (2008, p153) conclude: "visual and musculoskelatal factors affected spatial and temporal anchoring phenomena in different ways: the former by making use of task-specific visual information available at the gaze anchored point, the latter by exploiting task-specific mechanical properties". It is possible that anchoring at locations north and south rather reflect motor properties of the task, as the direction of the acceleration changes at those locations. This could be interpreted as a precedence of anatomical constraints in those conditions. In conditions where we find anchoring in other locations, visual-spatial constraints might be more prominent. This line of thinking is in accordance with recent attempts to disentangle how anatomical and spatial constraints interact, rather than asking which one dominates the other (Amazeen, DaSilva, & Amazeen, 2008; Li et al., 2004; Carson, 2005). Additionally, we suggest that visual setups that formed good Gestalts, like parallel/in-phase conditions in Experiment 2, had lower processing demand of the visual display, which promoted better performance. Hence, these conditions showed less sensitive to anchoring.

5.2.4 Egocentric Frame of Reference

Movement direction in reference to the body seems to be perceptual salient. We suggest that this is the case because participants use an egocentric Frame of Reference (FoR) for encoding and representing the position of the hand and its visual effect as well as the stimulus (Berthoz, 2000). An egocentric FoR implies that events are encoded in body-centered relations. It is a rather basic coding mode compared to allocentric FoR. Most animals are capable of egocentric coding and it is the FoR that infants use first, while allocentric FoR develops later. Infants start using visible spatial reference frames at the age of 16 months (Huttenlocher, Newcombe, & Sandberg, 1994) but this skill is not fully developed to a level comparable to adults until the age of 9 (Sandberg, Huttenlocher, & Newcombe, 1996). It might even be more efficient in terms of cognitive load as egocentric spatial coding requires only a subsystem of the processing resources of the allocentric condition (Zaehle et al., 2007).

This benefit of stimulus and feedback moving in the same direction in reference to the body might be comparable to mirror symmetry of the two limbs in bimanual coordination. As only one hand is used, it might not be theoretically correct to talk about an egocentric constraint. However, the body is the center of our world. Everything we experience in the extra-corporeal environment is evaluated and measured. Our perception builds an image of the extracorporeal world that is spread out around us in which we move and act, but we always keep a self-centered perspective. It can be expected that we process/categorize movements of our limbs in a similar self-centered way, i.e. whether the movement goes towards or away from the body.

5.2.5 Prediction and Internal Models

Our participants produced a very stable positive bias in their coordination performance, meaning that they were slightly but constantly ahead of their ideal position. We interpret this as evidence of predictive motor planning (Schütz-Bosbach & Prinz, 2007). This interpretation fits with simulation data by Neilson et al. (1995). The authors matched data of six participants who performed a tracking task to data computed by a simulator. The participants' data was best reproduced by a simulator using a predictive algorithm. These results provide convincing evidence that the

CNS tries to compensate for time delays caused by conduction or processing times by predicting future positions of the target. In other words, in order to experience subjective synchrony on a central level, prediction is used to give action a head start. Comparable results and interpretations are also known from tapping literature, describing the so called negative asynchrony (Aschersleben, 2002; Aschersleben & Prinz, 1995).

The neural processes underlying motor control are illustrated by internal models which combine predictors and controllers (Frith et al., 2000; Wolpert, 1997). While the predictor or *forward model* (Wolpert & Flanagan, 2001) predicts the outcome of executed motor commands, the controller or *inverse model* provides the motor commands necessary to achieve the desired results. Conscious access to these models is limited as humans are aware of the intended goals but not of the motor commands that take us there or the sensory feedback about the state of the system (Frith et al., 2000). It is suggested that this lack of awareness is beneficial for dealing successfully with sensorimotor transformations, as studied in tooluse (Müsseler & Sutter, 2009) (for a discussion of awareness in our participants see also 5.2.6.). For our paradigm, we assume that the transformations were integrated into the internal models as we find a positive bias in our transformed trials as well. This interpretation is not challenged by our finding that coordination control obviously suffers from the presence of a transformation. Forward and inverse models can be adapted independently to new task demands. Flanagan et al. (2003) showed that prediction learns faster than control. According to these authors, our motor system is able to predict an object faster than it is able to control it. We assume that participants could have achieved better results in some of our tasks if they had been given the time to train their controllers. It is, however, unlikely that performance with transformed feedback will be as accurate as performance with regular feedback, as the transformation induces cost in terms of additional cognitive load which show themselves in reduced accuracy.

5.2.6 Awareness of the Transformations

Participants had very little or no conscious access to the transformations. As our questionnaires revealed, they misjudged their performance and their ability to deal with the transformation, most drastically so in Experiment 5. These observations, together with the main finding of our study that coordination takes place between stimulus and visual feedback, form a picture of unimanual continuous coordination that is in accordance with both the ideomotor principle and studies on the poor awareness of our actual movements when confronted with visuo-motor or tool-use transformations. As mentioned above, the ideomotor principle could explain why participants focus on the more distal visual effects, because it is these visual effects on the screen that they are instructed to and which the anticipate. Research on visuo-motor transformation showed very constantly that participants are unaware of what their hands are actually doing when they are paying attention to modified visual feedback (Fourneret & Jeannerod, 1998; Koblich & Kircher, 2004) and do not acquire explicit knowledge of the transformations they are exposed to (Heuer & Hegele, 2008). It has been argued that this lack of awareness or uncertainty of our actual movements is central to being able to adapt flexibly to a variety of transformations and is highly beneficial for handling tools effectively (Müsseler & Sutter, 2009).

5.2.7 Symmetry

Symmetry is a very prominent feature in our visual world (Mechsner, 2003). In bimanual coordination, we find benefit for mirror symmetric movements (Mechsner et al., 2001; Swinnen, Jardin, et al., 1997). There is even evidence suggesting a special mechanism tuned for visual symmetry by the human visual system (Niimi, Watanabe, & Yokosawa, 2008). In our experiments however, we never found a benefit for conditions that resulted in visual symmetry on the screen compared to parallel conditions. One possible but unlikely explanation would be that because of poor accuracy, performance was not symmetric enough to still be perceived as symmetric and bring forth a symmetry benefit.

Another difference to bimanual studies is the fact that stability of the anti-phase pattern depends on the current rotation instruction. While performance accuracy is reduced in parallel/anti-phase trials compared to parallel/in-phase trials, participants still spent most of the time in the pattern instructed. In symmetry/anti-phase trials however, participants actually perform symmetry/in-phase patterns, i.e. they spent most of the time in the pattern contrary to the instructed one. This is in contrast to Swinnen, Jardin, et al. (1997) bimanual study who found phase switches in 75% of their symmetry/anti-phase trials [1], which was the least stable condition and most vulnerable to phase transitions, but they also found transitions in 44% of the parallel/anti-phase trials. The performance in symmetry/anti-phase trials did not change with inceasing speed, unlike in bimanual tasks, where participants switch into in-phase patterns with higher speed demands (Kelso, 1984). Our participants produced the contrary pattern even at the slowest speed levels.

5.2.8 Model of the Experimental Cycle

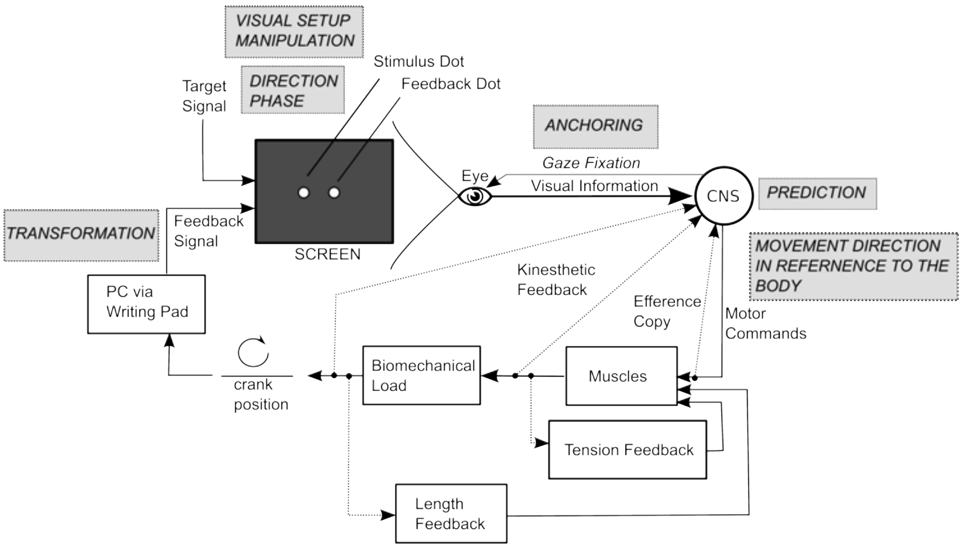

Figure 5.1: Revised Model (see Figure 1.1.) of the action-perception-cycle of the paradigm used incorporating the factors we manipulated or found to be crucial to our task in the gray boxes.

In the following paragraph, we will come back to the model introduced in Chapter 1.1. We will go through the experimental perception-action-cycle again, this time incorporating the results of our experiments (see Figure 5.1). We will start with the visual input from the screen. Visual information about the position of the stimulus and the feedback dot was transfered to the CNS via the retina. We interpret

[1] Swinnen, Jardin, et al. (1997) used different labels from ours for their conditions: symmetry/anti-phase corresponds to their Xanti/Yanti, parallel/anti-phase corresponds to their Xin/Yanti

our anchoring results as evidence that the CNS adjusts gaze fixation depending on the instruction and the current position of stimulus and feedback. On the basis of the visual information, the CNS predicts both the upcoming position of the stimulus as well as the corresponding position of the feedback dot. Taking the transformation into account, the CNS generates motor commands to activate arm muscles. Activated muscles contract and move the arm and thus also the crank. Information about the state of the system, i.e. the resulting muscle length, tension and joint angle goes back to the CNS. Situations where the gist of this information changes seem to be of special salience, like when movement direction in refence to the body changes. While the arm moves away from the body, the triceps contracts, reducing its length while tension builds up. Its antagonist, the biceps, relaxes, its tension weakens while its length increases. When movement direction changes to towards the body, the opposite pattern of information is generated. Now the biceps contracts while the triceps relaxes. It makes sense that changes like this offer themselves as opportunities to subdivide movements in order to control their accuracy and timing. To close the cycle, the information about the position of the crank (which equals the hand) is recorded by the writing pad and transfered to the PC. Here the transformation is applied before the new feedback position is displayed on the screen. Although, all our manipulations are established in the external part of the experimental cycle, they enter the internal part via perception. Some of them are consciously available, like rotation and phase instructions and the manipulation of the visual setup. The visuo-motor transformation, on the other hand, does not seem to be available to the participants even though it is integrated into motor planning.

5.3 Practical Implications

As in any experimental study, ecological validity suffers from the shortcomings that lie in the very nature of an experimental setting. We try to control for everything because we need to make sure that our effects are due to the manipulations of our experimental conditions. For our study, we chose a simple task of turning a crank handle with very limited context information. Even though participants did not reach perfection, they unanimously found the task very boring, while strenuous. Even though our task gives valuable insight into the mechanisms of motor control of continuous movements, it is not a task we will be likely to face in real life. Still, the interplay of the various factors we found to affect coordination even in this reduced setting gives us an idea of the complex processes the motor system administrates when coordinating our movements with events in the real world. There we find a much wider variety of distractions in terms of context and auditive and visual information that need to be evaluated and incorporated for successful coordination to take place.

However, the results of our experiments have some implications for real life situations. On the basis of our results, we suggest that in the design of control displays for complicated machines like airplanes, one should take care that processes that belong together or should be monitored together should be displayed close to each other and horizontally aligned. In the construction of tools like those for endoscopic surgery if transformations can not be avoided, they should be kept as small and as constant as possible. As we showed in Experiment 4, small transformations have less effect on performance accuracy, even though this need not be true for every kind of transformation (see Experiment 5). By keeping the transformation constant, users will be able to benefit from training effects without the need to periodically update on the current transformation.

If different tools have to be used together, the transformations they introduce should be the same, e.g. by placing the pivotal points of two levers at the same position or by technically reducing or enlarging them. This is all the more important if speeded responses are required or if users are not expected to be trained in handling the transformation. As participants are quite unable to judge the quality of their movements correctly, it might be advisable to set up some external, perhaps digital, control with sensitive devices where coordination accuracy or precise adjustment is necessary. Another way to increase awareness of the coordination accuracy is to embed target signals in an environment that facilitates spatial localization. One could think of employing visual grids or scales. The less context information there is (like the black screen in our paradigm), the less precise coordination will be.

5.4 Methodical Issues

With a measuring point every 10 ms, every trial produced a substantial amount of data. The measures we used to reduce this into interpretable statistical data were inspired by other publications like Tomatsu and Ohtsuki (2005); Mechsner et al.

(2001) and, of course, are only a sample of the possible measures. Especially for the anchoring analysis, we discussed, and in some cases conducted, a number of other possible calculations, like larger or smaller number of sections (e.g. dividing the circle into 4 instead of 24 sections) using a sliding window of overlapping sections to track the participants progress on the trajectory. For the sake of clarity and to minimize recurring information, we reduced the measures and calculations to the ones presented in the experimental section of this work. We tried to choose the measures that fitted best to answer our research questions. For instance, measure IM, which we interpret as a rather spatial measure, i.e. whether participants uphold the patterns instructed, could be also interpreted as a measure of the participants' timing. This is because if participants are able to produce the instructed visual pattern, they are also able to adjust the speed of their movements to that of the stimulus, which could also be regarded as a visual pace maker in this context.

5.5 Open questions

It is possible that the positive bias we found in the Constant Errors is due to the fact that participants used their right hand to perform the task. It has been reported that, with right-handed participants, the right hand leads the left hand in bimanual tasks (Roerdink et al., 2005). To test this, one could ask participants to perform the task with their non-dominant hand. However, a dramatic drop in performance is to be expected under these conditions.

We could only generate superficial knowledge about how participants experienced the task. Deeper insight could be generated by on-line reports on presence and impact of the transformation. This could also provide more detailed insight into how participants experienced the task and how they handled the transformation, especially for tasks like mirror transformations, where participants fail without noticing.

Although Experiment 6 opens the question whether visual or motor speed is the reason behind the observed speed-accuracy-trade-offs, we cannot answer this question. As we discussed in chapter 4.3, the influence of the transformation on the performance pattern is too strong to draw valid conclusions. With the current paradigm a separation of motor and visual speed would always need a transformation, which would again prevent insight. A way to circumvent this would be to set up a perceptual control experiment of some sort to study visual speed and compare this to a motor task.

Our results on anchoring, while interesting, are inconsistent and leave open the question of whether we measured visual (i.e. gaze direction) or musculoskelatal (i.e. wrist posture) components of anchoring. We found evidence of both feedback and movement related anchoring but our results fail to systematically show which occurs under what circumstances. We analyzed anchoring on the basis of the behavioral data produced by the hand. For more thorough investigation of the matter, additional use of eye-tracker technology seems highly advisable. This might enable us to separate visual anchoring from muskuloskeltal anchoring or at least show in detail where participants focus their gaze and whether they use different foci in the different visual setups and conditions. For musculoskelatal anchoring, a potentiometer to measure the angular position of the wrist might be useful.

5.6 Conclusion

This work was motivated by the question whether coordination of unimanual continuous movements with external events functions as movement-stimulus coordination or effect-stimulus coordination. In addition, we wanted to investigate which task characteristics are beneficial or disruptive for coordination performance. We conclude that action-to-event coordination in unimanual continuous tasks functions predominantly in terms of coordination of the stimulus to the visual feedback of the movement. Visual setup, combining the visual movement pattern instructed and the spatial arrangement of visual feedback and stimuli had an impact on coordination performance as did the presence, nature and magnitude of visuomotor-transformation between the actual hand movement and its visual feedback. Transformations are incorporated into motor planning but most of the time are not consciously available to the actor. The present work presents an investigation of the influence of visual context and visuomotor-transformations in coordination tasks and offers an insight into the the complex interplay of perception and action in this field of research.

References

Adams, J. A. (1971). A closed-loop theory of motor learning. *Journal of Motor Behavior*, *3*, 111-149.

Adams, J. A. (1977). Feedback theory of how joint receptors regulate the timing and positioning of a limb. *Psychological Review*, *84*(6), 504-523.

Alaerts, K., Levin, O., & Swinnen, S. P. (2007). Whether feeling or seeing is more accurate depends on tracking direction within the perception-action cycle. *Behavioral Brain Research*, *178*, 229-234.

Albert, N. B., & Ivry, R. B. (2009). The persistence of spatial interference after extended training in a bimanual drawing task. *Cortex*, *45*, 377-385.

Amazeen, E. L., DaSilva, F., & Amazeen, P. G. (2008). Visual-spatial and anatomical constraints interact in a bimanual coordination task with transformed visual feedback. *Experimental Brain Research*, *191*, 13-24.

Aschersleben, G. (2002). Temporal control of movements in sensorimotor synchronization. *Brain and Cognition*, *48*, 66-79.

Aschersleben, G., & Prinz, W. (1995). Synchronizing actions with events: The role of sensory information. *Perception & psychophysics*, *57*(3), 305-317.

Bedford, F. L. (1994). Of computer mice and men. *Current Psychology of Cognition*, *13*(4), 405-426.

Beek, P. (1989). *Juggling dynamics.* Unpublished doctoral dissertation, Free University Press, Amsterdam.

Beers, R. J. van, Wolpert, D. M., & Haggart, P. (2002). When feeling is more important than seeing in sensorimotor adaption. *Current Biology*, *12*, 834-837.

Berthoz, A. (2000). *The brain's sense of movement* (S. M. Kosslyn, Ed.). Harvard University Press.

Bingham, G., Schmidt, R., & Zaal, F. T. (1999). Visual perception of the relative phasing of human limb movements. *Percept Psychophys*, *61*, 246-258.

Bingham, G., Zaal F.T.J.M., Shull, J., & Collins, D. (2001). The effect of frequency on the visual perception of relative phase and phase variability of two oscillating objects. *Experimental Brain Research*, *136*, 543-552.

Bock, O., & Burghoff, M. (1997). Visuo-motor adaption: evidence for a distributed amplitude control system. *Behavioral Brain Research*, *89*, 267-273.

Bogaerts, H., Buekers, M. J., Zaal, F. T., & Swinnen, S. P. (2003). When visuomotor incogruence aids motor performance: the effect of percieving motion structures during transformed visual feedback on bimanual coordination. *Behavioral Brain Research*, *138*, 45-57.

Bramble, D. M., & Lieberman, D. E. (2004). Endurance running and the evolution of homo. *Nature*, *432*, 345-352.

Brenner, E., & Smeets, J. B. J. (2003). Fast corrections of movements with a computer mouse. *Spatial vision*, *16*, 365-376.

Buekers, M. J., Bogaerts, H. P., Swinnen, S. P., & Helsen, W. F. (2000). The synchronization of human arm movements to external events. *Neuroscience Letters*, *290*, 181-184.

Byblow, W. D., Carson, R. G., & Goodman, D. (1994). Expressions of asymmetries and anchoring in bimanual coordination. *Human Movement Science*, *13*, 3-28.

Byblow, W. D., Chua, R., & Goodman, D. (1995). Asymmetries in coupling dynamics of perception and action. *Journal of Motor Behavior*, *27*(2), 123-137. (nochmal lesen)

Byblow, W. D., Summers, J., Semjen, A., Wuyts, I., & Carson, R. (1999). Spontaneous and intentional pattern switching in a multisegmental bimanual coordination task. *Motor Control*, *3*(4), 372-93.

Börjesson, E., & Ahlström, U. (1993). Motion structure in five-dot patterns as a determinant of perceptual grouping. *Perception & Psychophysics*, *53*(1), 2-12.

Carson, R. G. (2005). Coordination dynamics: issues and trends. In V. Jirsa & J. Kelso (Eds.), (chap. Governing coordination: why do muscles matter?). Springer-Verlag, Berlin.

Carson, R. G., Thomas, J., Summers, J. J., Walters, M. R., & Semjen, A. (1997). The dynamics of bimanual circle drawing. *The Quarterly Journal of Experimental Psychology*, *50(3)*, 664-683.

Craig, J. C. (2006). Visual motion interferes with tactile motion perception. *Perception*, *35*, 351-367.

Desmurget, M., Pelisson, D., Rossetti, Y., & Prablanc, C. (1998). From eye to hand: planning goal-directed movements. *Neuroscience and Biobehavioral Reviews*, *22*(6), 761-788.

Fink, P. W., Foo, P., Jirsa, V. K., & Kelso, J. A. S. (2000). Local and global stabilzation of coordination by sensory information. *Experimental Brain Research*, *134*, 9-20.

Fitts, P. M. (1954). The information capacity of the human motor system in controling the amplitude of movement. *Journal of Experimental Psychology*, *47*(6), 381-391.

Flanagan, J. R., & Rao, A. K. (1995). Trajectory adaption to a nonlinear visuomotor transformation : Evidence of motor planning in visually perceived space. *Journal of Neurophysiology*, *74*(5), 2174-2178.

Flanagan, J. R., Vetter, P., Johansson, R. S., & Wolpert, D. M. (2003). Prediciton precedes control in motor learning. *Current Biology*, *13*, 146-150.

Fleury, M., Bard, C., Gagnon, M., & Teasdale, N. (1992). Coincidence-anticipation timing the perceptual-motor interface. *Advances in Psychology*, *85*, 315-334.

Fourneret, P., & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia*, *36*(11), 1133-1140.

Franz, E., Zelaznik, H. N., & McCabe, G. (1991). Spatial topological constraints in a bimanual task. *Acta Psychologica*, *77*(2), 137-51.

Frith, C. D., Blakemore, S.-J., & Wolpert, D. M. (2000). Abnormalities in the awareness and control of action. *Philosophical Transitions of the Royal Society of London*, *355*, 1771-1788.

Ghahramani, Z., Wolpert, D. M., & Jordan, M. I. (1996). Generalization to local remappings of the visuomotor coordinate transformation. *The Journal of Neuroscience*, *16*(21), 7085-7096.

Guedon, O., Gauthier, G., Cole, J., Vercher, J.-L., & Blouin, J. (1998). Adaption in visuomanual tracking depends on intact proprioception. *Journal of Motor Behavior*, *30*(3), 234-248.

Haken, H., Kelso, J. A. S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biol. Cybern.*, *51*, 347-356.

Heuer, H. (1993). Structural constraints on bimanual movements. *Psychological Research*, *55*, 83-98.

Heuer, H., & Hegele, M. (2007). Learning new visuo-motor gains at early and late working age. *Ergonomics*, *50*(7), 979-1003.

Heuer, H., & Hegele, M. (2008). Constraints on visuo-motor adaption depend on the type of visual feedback during practice. *Experimental Brain Research*, *185*, 101-110.

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (tec): a framework for perception and action planning. *Behavioral and Brain Sciences*, *24*, 849-937.

Huttenlocher, J., Newcombe, N., & Sandberg, E. (1994). The coding of spacial location in young children. *Cognitive Psychology*, *27*, 115-148.

Huys, R., Williams, A. M., & Beek, P. (2005). Visual perception and gaze control in judging versus producing phase relations. *Human Movement Science*, *24*, 403-428.

Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., Pütz, B., et al. (2000). Human cereballar activity reflecting an aquired internal model of a new tool. *Nature*, *403*, 192-195.

James, W. (1890). *The principles of psychology* (Vol. Volume Two). Dover Publications, Inc. : New York.

Jordan, M. I. (1996). Handbook of perception and action: motor skills. In H. Heuer & S. Keele (Eds.), (Second Edition ed., p. 71-118). New York: Academic Press.

Kagerer, F. A., Contreras-Vidal, J. L., & Stelmach, G. E. (1997). Adaption to gradual as comapred with sudden viduo-motor distortions. *Experimental Brain Research*, *115*, 557-561.

Kelso, J. A. S. (1984). Phase transitions and critical behavior in human bimanual coordination. *Am. J. Physil. (Regulatory Integrative Comp. Physiol)*, *246*(15), R1000-R1004.

Kelso, J. A. S. (1995). *Dynamic patterns: The self-organization of brain and behavior.* (J. Kelso, Ed.). MIT Press.

Kelso, J. A. S., Southard, D. L., & Goodman, D. (1979). On the coordination of two-handed movements. *Journal Of Experimental Psychology: Human Perception and Performance*, *5*(2), 229-238.

Killeen, P., & Weiss, N. (1987). Optimal timing and the weber function. *Psychological Review*, *94*(4), 455-468.

Knuf, L., Aschersleben, G., & Prinz, W. (2001). An analysis of ideomotor action. *Journal of Experimental Psychology: General*, *130*(4), 779-798.

Koblich, G., & Kircher, T. T. (2004). Deceiving oneself about being in control: conscious detection of changes in visuomotor coupling. *Journal Of Experimental*

Psychology: Human Perception and Performance, *30*(4), 657-666.

Künnapas, T. M. (1955). An analysis of the "vertical-horizontal illusion". *Journal of Experimental Psychology*, *49*, 134-140.

Lepper, M., Massen, C., & Prinz, W. (2008). What to do and how to do it: sequence learning of action effects and transformation rules. *Acta Psychologica*, *128*(1), 139-52.

Li, Y., Levin, O., Carson, R. G., & Swinnen, S. P. (2004). Bimanual coordination: constraints imposed by the relative timing of homologous muscle activation. *Experimental Brain Research*, *156*, 27-38.

Lotze, H. (1852). *Medicinische psychologie oder physiologie der seele*. Leipzig: Weidmannsche Buchhandlung.

Massen, C., & Prinz, W. (2007). Programming tool-use actions. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 692-704.

Mechsner, F. (2003). Gestalt factors in human movement coordination. *Gestalt Theory*, *25*(4), 225-245.

Mechsner, F. (2004). A psychological approach to human voluntary movements. *Journal of Motor Behavior*, *36*(4), 355-370.

Mechsner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001). Perceptual basis of bimanual coordination. *Nature*, *414*, 69-73.

Metzger, W. (1954). Aktuelle probleme der gestaltpsychologie. In R. Meili (Ed.), (p. 3-15). Hans Huber, Bern.

Mohler, B. J., Thompson, W. B., Creem-Regehr, S. H., Pick Jr, H. L., & Warren Jr, W. H. (2007). Visual flow influences gait transition speed and preferred walking speed. *Experimental Brain Research*, *181*, 221-228.

Müsseler, J., & Sutter, C. (2009). Perceiving one's own movements when using a tool. *Consciousness and Cognition*, *18*, 359-365.

Neilson, P. D., Neilson, M. D., & O'Dwyer, N. J. (1995). Motor control and sensory motor integration: Issues and directions. In D. Glencross & J. Piek (Eds.), (p. 97-140). Elsevier Science.

Nicoletti, R., & Umilta, R. (1989). Splitting visual space with attention. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(1), 164-169.

Niimi, R., Watanabe, K., & Yokosawa, K. (2008). The dynamic-stimulus advantage of visual symmetry perception. *Psychological Research*, *72*, 567-579.

Obhi, S. S., & Haggard, P. (2004). The relative effects of external spatial and motoric factors on the bimanual coordination of discrete movements. *Experimental Brain Research*, *154*, 399-402.

Oliveira, S. Cardoso de. (2002). The neuronal basis of bimanual coordination: recent neurophysiological evidence and functional models. *Acta Psychologica*, *110*(2-3), 139-59.

Palluel-Germain, R., Boy, F., Orliaguet, J., & Coello, Y. (2004). Visual and motor constraints on the trajectory planning in pointing movements. *Neuroscience Letters*, *372*, 235-239.

Prinzmetal, W., & Gettleman, L. (1993). Vertical-horizontal illusion: one eye is better than two. *Perceptional Psychophysics*, *53*(1), 81-8.

Rieger, M., Knoblich, G., & Prinz, W. (2005). Compensation for and adaption to changes in the environment. *Experimental Brain Research*, *163*, 487-502.

Rieger, M., Verwey, W. B., & Massen, C. (2008). The effect of continuous, nonlinearly transformed visual feedback on rapid aiming movements. *Experimental Brain Research*, *191*(1), 1-12.

Robertson, S., Zelaznik, H., Lantero, D., Bojczyk, K., Spencer, R., Doffin, J., et al. (1999). Correlations for timing consistency among tapping and drawing tasks: evidence against a single timing process for motor control. *Journal Of Experimental Psychology: Human Perception and Performance*, *25*(5), 1316-30.

Roerdink, M., Ophoff, E. D., Peper, C. L. E., & Beek, P. J. (2008). Visual and musculoskeletal underpinnings of anchoring in rhythmic visuo-motor tracking. *Experimental Brain Research*, *184*, 143-156.

Roerdink, M., Peper, C., & Beek, P. (2005). Effects of correct and transformed visual feedback on rhythmic visuo-motor tracking: Tracking performance and visual search behavior. *Human Movement Science*, *24*, 379-402.

Rosenbaum, D. A., & Gregory, R. W. (2002). Development of a method for measuring movement-related effort: biomechanical considerations and implications for fitts' law. *Experimental Brain Research*, *142*, 365-373.

Salter, J. E., Wishart, L. R., Lee, T. D., & Simon, D. (2004). Perceptual and motor contributions to bimanual coordination. *Neuroscience Letters*, *363*, 102-107.

Sandberg, E., Huttenlocher, J., & Newcombe, N. (1996). The development of hierarchical representation of two-dimensional space. *Child Development*, *67*(3), 721-739.

Schmidt, R. A. (1975). A schema theory of discrete motor skill learning. *Psychological Review*, *82*(4), 225-260.

Schmidt, R. A., Zelaznik, H., Hawkins, B., Frank, J. S., & Quinn, J. T. J. (1979). Motor-output variability: A theory for the accuracy of rapid motor acts. *Psychological Review*, *86*(5), 415-451.

Schütz-Bosbach, S., & Prinz, W. (2007). Prospective conding in event representation. *Cognitive Process*, *8*, 93-102.

Seidler, R., Bloomberg, C., & Stelmach, G. E. (2001). Patterns of transfer of adaption among body segments. *Behavioral Brain Research*, *122*, 145-257.

Semjen, A., Summers, J., & Cattaert, D. (1995). Hand coordination in bimanual circle drawing. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(5), 1139-1157.

Spencer, R. M., Zelaznik, H. N., Diedrichsen, J., & Ivry, R. B. (2003). Disrupted timing of discontinuous but not continuous movements by cerebellar lesions. *Science*, *300*, 1437-1439.

Sutter, C. (2007). Sensumotor transformation of input devices and the impact on practice and task difficulty. *Ergonomics*, *50*(12), 1999-2016.

Swinnen, S. P., Jardin, K., Meulenbroek, R., Dounskaia, N., & Hofkens-Van Den Brandt, M. (1997). Egocentric and allocentric constraints in the expression of patterns of interlimb coordination. *Journal of Cognitive Neuroscience*, *9*(3), 348-377.

Swinnen, S. P., Lee, T. D., Verschueren, S., Serrien, D., & Bogearts, H. (1997). Interlimb coordination: learning and transfer under different feedback conditions. *Human Movement Science*, *16*, 749-785.

Tomatsu, S., & Ohtsuki, T. (2005). The effect of transformed feedback on bimanual circling movement. *Experimental Brain Research*, *166*, 277-286.

Verwey, W. B., & Heuer, H. (2007). Nonlinear visuomotor trasnformations: Locus and modularity. *The Quarterly Journal of Experimental Psychology*, *60*(12), 1629-1659.

Weigelt, C., & Oliveira, S. Cardoso de. (2003). Visuomotor transformations affect bimanual coupling. *Experimental Brain Research*, *148*, 439-450.

Wertheimer, M. (1923). Untersuchungen zur lehre von der gestalt. *Psychologische Forschung*, *4*, 301-350.

Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005a). Human movement coordination implicates relative direction as the information for relative phase. *Experimental Brain Research*, *164*, 351-361.

Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005b). Perceptual coupling in rhythmic movements coordination: stable perception leads to stable action. *Experimental Brain Research*, *164*, 517-528.

Wimmers, R. H., Beek, P. J., & Wieringen, P. C. van. (1992). Phase transitions in rhythmic tracking movements: A case of unilateral coupling. *Human Movement Science*, *11*, 217-226.

Wohlschläger, A., Gattis, M., & Bekkering, H. (2003). Action generation and action perception in imitation: an instance of the ideomotor principle. *Philosophical Transitions of the Royal Society of London*, *358*, 501-515.

Wolpert, D. M. (1997). Computational approaches to motor control. *Trends in Cognitive Science*, *1*(6), 209-216.

Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology*, *11*(18), R729-R732.

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*, 1212-1217.

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). Are arm trajectories planned in kinematik or dynamic coordinate? an adation study. *Experimental Brain Research*, *103*, 460-470.

Wulf, G., & Prinz, W. (2001). Directing attention to movement effects enhances learning: A review. *Psychonomic Bulletin & Review*, *8*(4), 648-660.

Zaal, F. T., Bingham, G., & Schmidt, R. (2000). Perception of mean relative phase and phase variability. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 1209-1220.

Zaehle, T., Jordan, K., Wüstenberg, T., Baudewig, J., Dechent, P., & Mast, F. W. (2007). The neural basis of the egocentric and allocentric spatial frame of reference. *Brain Research*, *1137*, 92-103.

Zelaznik, H. N., Spencer, R. M. C., & Ivry, R. B. (2002). Dissociation of ecplicit and implicit timing in repetitive tapping and drawing movements. *Journal Of Experimental Psychology: Human Perception and Performance*, *28*(3), 575-588.

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Bibliographische Darstellung

Dietrich, Sandra

COORDINATION OF UNIMANUAL CONTINUOUS MOVEMENTS WITH EXTERNAL EVENTS

Dissertation
Fakultät für Biowissenschaften, Pharmazie und Psychologie der Universität Leipzig

115 Seiten, 103 Literaturangaben, 26 Abbildungen, 10 Tabellen

Referat

This dissertation focuses on the coordination of unimanual continuous movements with external events and the question whether coordination takes place between the stimulus and the actual movement or between the stimulus and the feedback of the movement in the environment. To study this issue, a circling paradigm that required participants to coordinate their hand movements with a continuously circling stimulus and allowed visuo-motor transformation, was used. In the first empirical part trajectories of stimulus and feedback were either presented next to each other, within each other or above/below each other. We varied the instructed coordination pattern and phase and dissociated movements and visual movement feedback by applying transformed feedback (180° phase shift). Results indicate that unimanual coordination follows the principle of vision-to-stimulus-coordination, but subtle effects of movement-to-stimulus-coordination were also observed.

In the remainder of the experiments, we used different types of transformations: different phase shifts, direction reversion and different gains. Results show that transformations though not consciously available are incorporated into motor planning while their effect on performance quality depends on their magnitude and nature.

To conclude, coordination of unimanual continuous movements relies heavily on the visual effect of the movement with performance quality depending on the visual presentation of stimulus and feedback and the magnitude and nature of the transformation between actual movement and feedback.

Zusammenfassung

Einleitung

Die Fähigkeit, Bewegungen mit Ereignissen im außerkörperlichen Raum zu koordinieren, wird durch anatomische Beschränkungen und eine sich ständig ändernde Umwelt bestimmt. Es stellt sich die Frage, an welcher Stelle des Wahrnehmungs-Handlungs-Zyklus der Abgleich zwischen Bewegung, wahrgenommenen Bewegungseffekten und externen Stimuli tatsächlich stattfindet.
Eine mögliche Hypothese wäre, dass die Handbewegung mit dem externen Stimulus koordiniert wird (Bewegung-Stimulus-Koordination), was bedeuten würde, dass Eigenschaften der Bewegung in ihrer Beziehung zum Stimulus (z.B. gleiche Bewegungsrichtung) wichtig für die Genauigkeit der Koordination sind. Im Gegensatz dazu könnte die wichtigere Beziehung zwischen Bewegungseffekten und dem externen Stimulus bestehen (Effekt-Stimulus-Koordination) und Übereinstimmungen auf dieser Ebene sollten die Koordinationsleistung verbessern.
Dies würde mit Vorhersagen des Ideomotorischen Prinzips (James, 1890; Lotze, 1852) übereinstimmen, welches aussagt, dass Handlungen durch die von ihnen intendierten Ergebnisse repräsentiert werden. Bereits vorhandene Studien in der Koordinationsforschung können im Sinne der Effekt-Stimulus-Koordination interpretiert werden (Mechsner et al., 2001; Roerdink et al., 2005). Es fehlt bisher jedoch eine Studie mit dem ausdrücklichen Ziel, Bewegung-Stimulus- und Effekt-Stimulus-Koordination für unimanuelle Bewegungen gegenüberzustellen. Dazu bedarf es außerdem eines Paradigmas, welches es erlaubt, Wahrnehmungs-Handlungs-Kreisläufe näher zu untersuchen und der Koordination förderliche bzw. hinderliche Bewegung-Stimulus- oder Effekt-Stimulus-Beziehungen zu identifizieren.
Das in dieser Arbeit verwendete Paradigma ist aus der bimanualen Forschung entliehen und wurde so modifiziert, dass es die genannten Anforderungen für unimanuale Versuchsanordnungen erfüllt. Die Aufgabe der Probanden bestand darin, das visuelle Feedback ihrer Handbewegung mit einem sich auf einer Kreisbahn bewegenden Stimulus zu koordinieren. Dafür erhielten sie Anweisungen bezüglich der zu erzielenden Bewegungsmuster (z.B. spiegelsymmetrisch oder parallel). Die Kongruenz zwischen Handbewegung und visuellem Feedback konnte durch das

Zwischenschalten von Transformationen manipuliert werden. Dadurch konnte bewusst eine Übereinstimmung zwischen Bewegung und Stimulus bzw. Feedback und Stimulus hergestellt werden, um zu prüfen, an welcher Stelle diese Übereinstimmungen förderlich für die Koordinationsleistung sind.
Ziel dieser Dissertation ist es also, Evidenz für das Vorherrschen von Bewegung-Stimulus- oder Effekt-Stimulus-Koordination bei kontinuierlichen unimanualen Bewegungen zu sammeln und Eigenschaften der Aufgabe zu identifizieren, welche für die Koordinationsleistung förderlich oder hinderlich sind.
Besonderes Augenmerk galt dabei der Symmetrie als perzeptueller Eigenschaft des visuellen Displays, die sich in bimanualen Studien als Prädiktor für die Qualität von Koordinationsleistungen abgezeichnet hat. So konnte mit Hilfe von spiegelsymmetrischem Feedback die Koordinationsleistung nicht-symmetrischer bimanualer Bewegungsaufgaben verbessert werden (Mechsner et al., 2001; Tomatsu & Ohtsuki, 2005). Es wird angenommen, dass es eine Neigung zu wahrgenommener Symmetrie gibt. Diese sollte sich auch in unserem unimanualen Paradigma zeigen.
Im ersten Teil der Arbeit (Experimente 1-3) lag der Schwerpunkt besonders auf der Untersuchung des Einflusses des visuellen Setups. Wenn verfügbar, so schein visuelles Feedback eine gewisse Dominanz als Informationsquelle sowohl über den Zustand des Systems, als auch über die Umwelt innezuhaben (Alaerts et al., 2007; Craig, 2006). Der Grund dafür mag darin liegen, dass visuelles Feedback zumeist leicht zugänglich ist und wenig Rauschen enthält (Wilson et al., 2005b, 2005a).
Um den Zusammenhang zwischen visuellem Feedback und tatsächlicher Bewegung näher zu untersuchen, wurden im zweiten Teil der Dissertation verschiedene Transformationen zwischen Feedback und Bewegung eingesetzt.

Zusammenfassung der wissenschaftlichen Ergebnisse

Die Ergebnisse der Experimente 1 bis 3 zeigten, dass die Koordination unimanualer Handbewegungen in unserem Paradigma im Sinne einer Effekt-Stimulus-Koordination funktioniert, da Übereinstimmungen zwischen Effekt und Stimulus bessere Leistungen hervorriefen, als Übereinstimmungen zwischen Bewegung und Stimulus. Die Probanden zeigten einen positiven Fehlerbias, d.h. sie waren ihren idealen Position eher voraus, was wir als Indiz für prädiktive Bewegungsplanung deuten. Durch die Anwesenheit einer Transformation leidet die Koordinationsgenauigkeit,

ohne dass sich die Probanden dessen bewusst waren. Die gleiche Bewegungsrichtung in Bezug auf den Körper (d.h. vom Körper weg vs. auf den Körper zu) schien eine wichtige Komponente der Koordinationsleistung für unser Paradigma zu sein. Probanden nutzen den Punkt, an dem diese Bewegungsrichtung wechselt, zur Synchronisation ihrer Bewegung mit dem Stimulus, vor allem in Abwesenheit anderer markanter Orientierungspunkte und mit steigender Aufgabenschwierigkeit. Im Gegensatz zu bimanualen Studien (Swinnen, Jardin, et al., 1997), in denen spiegelsymmetrische Muster allgemein mit besserer und stabilerer Leistung einhergehen, konnten wir keinen Vorteil für spiegelsymmetrische Muster im Vergleich mit parallelen Mustern finden. Im Gegenteil, unter bestimmten Bedingungen konnten symmetrische Muster sogar schwerer aufrechtzuerhalten sein als parallele Muster. Allerdings können wir zeigen, dass Probanden in denjenigen Aufgaben erfolgreich sind, welche die besten und stabilsten Muster im Sinne der Gestaltlehre formen (Bogaerts et al., 2003; Mechsner, 2003).
Um die Bedeutung der Beziehung zwischen tatsächlicher Bewegung und visuellen Bewegungseffekten näher zu untersuchen wurden im zweiten Teil der Arbeit unterschiedliche Transformationen eingesetzt. Nicht nur das physikalische Ausmaß der Transformation, sondern auch deren wahrgenommene Konsequenzen hatten Einfluss auf die Qualität der Koordinationsleistung mit dieser Transformation. Mit Phasenverschiebungen unterschiedlicher Größe (Experiment 4) konnte der Eindruck erweckt werden, das Feedback eile der Hand voraus bzw. laufe der Hand hinterher, wobei Vorauseilen mit besserer Koordinationsleistung einherging. In einem weiteren Experiment wurde die motorische Geschwindigkeit durch eine Verstärkungstransformation von der visuellen Geschwindigkeit getrennt (Experiment 6). Dabei konnte in mehreren Stufen entweder eine schnelle Handbewegung in einer langsamen visuellen Bewegung resultieren (Verlangsamung) oder umgekehrt eine langsame Handbewegung in einer schnellen visuellen Bewegung (Verschnellerung).
Die Koordinationsleistung wurde weder allein von der motorischen noch der visuellen Geschwindigkeit bestimmt, sondern beide beeinflussen interdependent die Leistung. Natürlich ist es möglich, durch Transformationen Bewegung und Feedback soweit zu trennen, dass Koordination nicht mehr möglich ist. Durch das Einschalten einer Transformation, welche die Bewegungsrichtung zwischen Hand und Feedback umkehrte, d.h. aus einer Handbewegung im Uhrzeigersinn wurde eine Feedbackbewegung entgegen den Uhrzeiger und umgekehrt, fiel die Leistung

der Probanden auf Zufallsnivau (Experiment 5). Interessant an diesem Ergebnis ist, dass sich die Probanden zum einen ihrer schwachen Leistungen nicht bewusst waren, diese Leistungen zum anderen durch eine direkte Instruktion auf die Transformation nicht verbessert wurden. Die Transformationen wurden auf einem Level in die Bewegungsplanung integriert, welches kognitiv nicht bewusst zugänglich und beeinflussbar ist.

Zusammenfassend lässt sich sagen, dass für die Koordination unimanualer kontinuierlicher Bewegungen im Sinne einer Effekt-Stimulus-Koordination funktioniert, d.h. die visuellen Bewegungseffekte sind maßgeblich für die Koordination mit dem externen Reiz. Die Genauigkeit der Leistung lässt sich durch die Manipulation der visuellen Präsentation von Stimulus und Feedback beeinflussen. Transformationen haben einen negativen Einfluss auf die Koordinationsleistung. Wie groß die durch sie entstehenden Kosten ausfallen, hängt von Art und Ausmaß der Transformation, sowie deren wahrgenommenen Eigenschaften und Qualitäten ab. Transformationen werden in gewissem Maße in die motorische Planung integriert, sind aber nicht bewusst zugänglich.

Summary

Introduction

The ability to coordinate movements with events in extracorporeal space is limited by anatomical constraints and an ever-changing environment. This raises the question at which point of the perception-action-cycle the adjustment between movement, perceived movement effects and external stimuli exactly happens.
One hypothesis would be that hand movement is coordinated with the external stimulus (movement-stimulus coordination), which would mean that properties of the movement relation to properties of the stimulus (e.g. same movement direction) are important for the accuracy of the coordination. In contrast, the important relation could be between movement effects and the external stimulus (effect-stimulus coordination) and matches between them would improve coordination performance. This would agree with predictions of the Ideomotor Principle (James, 1890; Lotze, 1852), which assumes that actions are represented in terms of their intended effects.

Existing studies in coordination research can be interpreted according to effect-stimulus-coordination (Mechsner et al., 2001; Roerdink et al., 2005, e.g.). What is missing up to now is a study with the explicit aim of comparing movement-stimulus coordination and effect-stimulus coordination for unimanual coordination. This requires an experimental paradigm which allows us to study perception-action cycles and identify movement-stimulus or effect-stimulus relations that are beneficial or disruptive for coordination.

The paradigm used in this work is borrowed from bimanual research and adapted to meet the requirements mentioned for unimanual research. Participants had to coordinate the visual feedback of their hand movements with a continuously circling stimulus. They received instructions on the intended movement patterns (symmetry vs parallel; in-phase vs anti-phase). Congruence between hand movements and their visual feedback could be manipulated by introducing transformations. Thereby, correspondences between movement and stimulus or feedback and stimulus could deliberately be created in order to study where this correspondences is beneficial for coordination performance.

The aim of this dissertation is to collect evidence for the dominance of movement-

stimulus or effect-stimulus-coordination in the coordination of unimanual movements and identify task characteristics which are beneficial or disruptive for coordination performance.

Special attention was given to symmetry as characteristic of the visual display which proved to be a predictor of performance quality in bimanual coordination studies. Thus, coordination performance of a non-symmetric movement task could be improved by mirror-symmetric feedback (Mechsner et al., 2001; Tomatsu & Ohtsuki, 2005). It is assumed that there is a general bias towards perceived symmetry. If this is correct this bias should also show itself in our unimanual paradigm.

In the first part of this dissertation, the focus was on the study of role of the visual display. If available, visual feedback seems to be the dominant source of information both about the state of the system and the environment (Alaerts et al., 2007; Craig, 2006). The reason for this might be that visual feedback is easily available and contains little noise (Wilson et al., 2005b, 2005a). In the second part of the dissertation, we employed different transformations in order to study the relationship between visual feedback and actual movement and its impact on movement performance.

Summary of the Experimental Findings

In the first empirical part of this work stimulus and visual feedback were presented horizontally (Experiment 1) or vertically aligned (Experiment 3) and on interleaved trajectories (Experiment 2). The results of Experiments 1 to 3 show that coordination of unimanual continuous movements functions as effect-stimulus coordination in our paradigm, as similarities between feedback and stimulus improved performance compared to similarities between movement and stimulus. Participants showed a positive bias, i.e. they were ahead of their ideal position, which we interpreted as evidence of predictive movement planning.

The presence of a transformation reduced coordination accuracy without participants being aware of it. Shared movement direction in reference to the body (i.e. towards or away from the body) seemed to be an important characteristic of coordination performance in our paradigm. Participants used the position at which this movement direction changes to synchronize their movements with the stimulus, especially in the absence of other salient points of reference and with increasing task difficulty.

In contrast to bimanual studies (Swinnen, Jardin, et al., 1997) where mirror symmetric patterns usually go along with stable performance, we did not find a benefit for mirror symmetric patterns compared to parallel patterns. On the contrary, under certain conditions symmetric patterns could be even harder to maintain than parallel patterns. We could show that participants were most successful in those conditions where the most stable Gestalts in the sense of the Gestalt theory (Bogaerts et al., 2003; Mechsner, 2003) were generated by feedback and stimulus.

In the second part of the dissertation we employed different transformations to study the relation between actual movement and visual feedback. Quality of the coordination performance was not only affected by the physical magnitude of the transformation but also by their perceived consequences. Phase shifts of different size (Experiment 4) evoked the impression of the feedback running ahead or trailing behind the hand. The impression of running ahead was more beneficial for performance.

In Experiment 6, motor speed was separated from visual speed by a gain transformation. In several steps, a faster hand movement could result in a slower visual movement or a slower hand movement could result in faster visual movements. Coordination performance was neither exclusively dependent on motor nor on visual speed, but both were mutually dependent.

We were able to separate movement and feedback until deliberate coordination is impossible. By employing a transformation that reversed the rotation between hand and feedback, i.e. a clockwise hand rotation resulted in an anti-clockwise feedback rotation, performance decayed to chance level (Experiment 5). Interestingly, participants were neither aware of their poor performance nor was performance improved by making the transformation transparent. Transformations are integrated into movement planning at a level that is not consciously available or controlled.

To conclude, coordination of unimanual continuous movements functions on terms of effect-stimulus coordination, i.e. visual movement effects are dominant for coordination with external events. Performance accuracy can be manipulated by the visual presentation of stimulus and feedback. Transformations reduce performance accuracy. How much performance suffers depends on the nature and magnitude of the transformation as well as its perceived characteristics. Transformations are integrated into motor planning but not consciously available.

Curriculum Vitae

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Veröffentlichungen

Dietrich, S., Rieger, M., & Prinz, W. (2008). Action-Effect Transformations in Unimanual Coordination. In , Abstracts of the Psychonomic Society (Abstracts of the Psychonomic Society, Vol. 13, p. 100). : Psychonomic Society Publication.

Dietrich, S., Rieger, M., & Prinz, W. (2008). Der Kontext visueller Bewegungseffekte beeinflusst die Koordinationsleistung.. In P. Khader, K. Jost, & H. Lachnit (Eds.), Beiträge zur 50. Tagung experimentell arbeitender Psychologen p. 125. Lengerich: Pabst Science Publishers.

Dietrich, S., Rieger, M., & Prinz, W. (2008). Visual-spatial layout contributes to unimanual coordination. International Journal of Psychology, 43(3/4), 450.

Dietrich, S., Rieger, M., & Prinz, W. (2007). The effect of transformed feedback on unimanual circling movements. In K. F. Wender, S. Mecklenbräuker, G. D. Rey, & T. Wehr (Eds.), Beiträge zur 49. Tagung experimentell arbeitender Psychologen p. 91. Lengerich: Pabst Science Publishers.

Vorträge

Dietrich, S., Rieger, M., & Prinz, W. (2008, March). Der Kontext visueller Bewegungseffekte beeinflusst die Koordinationsleistung. Tagung experimentell arbeitender Psychologen (TeaP), Phillips-Universität Marburg, Germany

Dietrich, S., Rieger, M., & Prinz, W. (2008, February). Effektrelevanz für die Koordination unimanueller kontinuierlicher Bewegungen . Workshop zum ideomotorischen Prinzip, Max Planck Institute for Human Cognitive and Brain Sciences & Psychologisches Institut der Universität Würzburg, Weimar, Germany

Dietrich, S., Rieger, M., & Prinz, W. (2007, March). Der Effekt von transformiertem Feedback auf unimanuelle Kreisbewegungen. Tagung experimentell arbeitender Psychologen, Universität Trier, Trier

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Hiermit erkläre ich,

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   - Professor Dr. Wolfgang Prinz, Max-Planck-Institut für Kognitions- und Neurowissenschaften Leipzig

   - Dr. Martina Rieger, Max-Planck-Institut für Kognitions- und Neurowissenschaften Leipzig

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