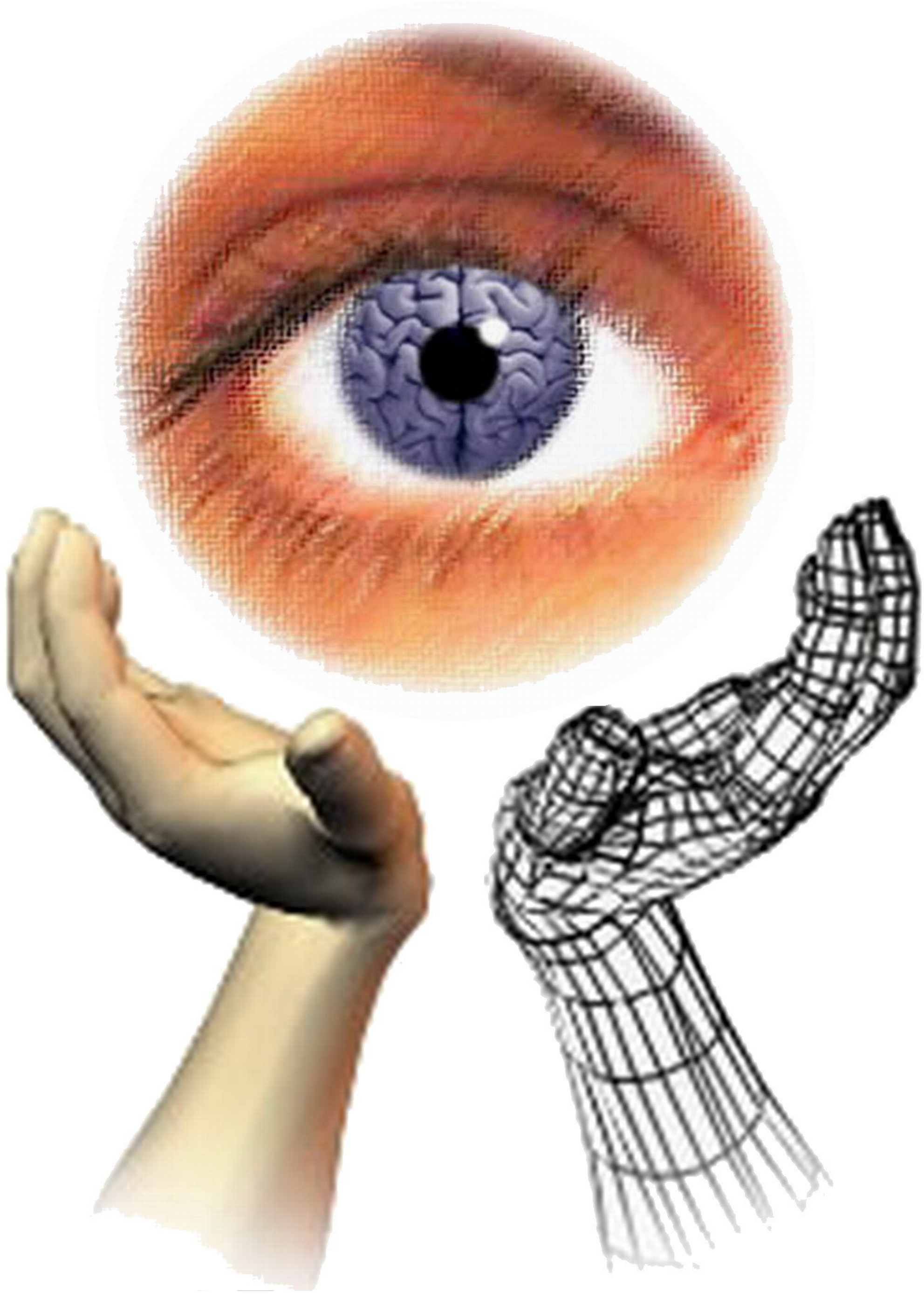

TRANSFER OF ADAPTATION ACROSS MOVEMENT CATEGORIES IN EYE HAND COORDINATION

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Declaration of Authorship

I certify that the dissertation at hand reports original work performed and completed by me during my Ph.D. project at the University. No other person's work has been used without due acknowledgement in the text of this document. The "Guidelines for Good Scientific Practice" (§9, Sec. 3) were adhered to in this dissertation. This work has never been submitted in this or similar form at this or any other domestic or foreign institution of higher learning in purpose of acquiring the doctor in philosophy.

Signature Date

Acknowledgements

I dedicate this work to my parents to thank them, because without them I would not have been able to do this. You have guided and taught me for so long (thirty years to be exact). Without your long-standing guidance and emotional support, I would not have seized as many opportunities as I did, or have the possibilities. Without you, I would never have attained the level of determination to the edge of stubbornness, strength and hardship to make it through life or through the vexing years of working towards a doctoral degree. Essentially, if it were not for the two of you, I would not be here, not in this world not at this spot in my life, thank you from the bottom of my heart you are the best parents anyone could possibly wish for, I could not have done this without you. Thank you!

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PREFACE

Movements and actions are a daily part of our life and many processes in the brain allow us to move or interact with our environment. The brain is hierarchical functionally segregated, enabling us to use several systems simultaneously. We see an object, and automatically we know where it is in space, in relation to our body, we can estimate its size and weight, we can reach for it, pick it up, and interact with it. The brain encodes visual scenes and perceptions of the body, translating them into neural signals and adjusting them to fit the specific situation we face and determines the needed or wanted action. The visuomotor system is a highly complex and interactive system, processing information of many other systems, such as visual, haptic and spatial information, hereby allowing us to perform such 'simple' acts as picking up a glass and drinking from it.

A popular way of investigating the visuomotor system is through adaptation studies, by distorting the visual or the sensory (proprioceptive) feedback. Such tasks allow us to discern a wide range of skills. Such as how much we rely on different feedback mechanisms, what we actually 'need' to plan or perform a movement and last but not least how flexible the visuomotor system actually is. The importance of adaptation relates to the needed flexibility of the human system. We need flexibility to cope with the large variety of situations we face in daily life.

The questions I asked focus on learning and transfer of skills in a normal and a distorted environment where human subjects draw simple lines and geometrical shapes. I wanted to see whether learning and adaptation to a distortion differed when performing different movements. Most studies using visuomotor distortion in such a way focused on pointing and reaching movements. The experiments described in the following chapters instead use (2D) movements or rather drawing movements. I asked students to perform simple and complex drawing tasks while applying a visuomotor distortion to their movement feedback, hereby expecting differences between the different movement types.

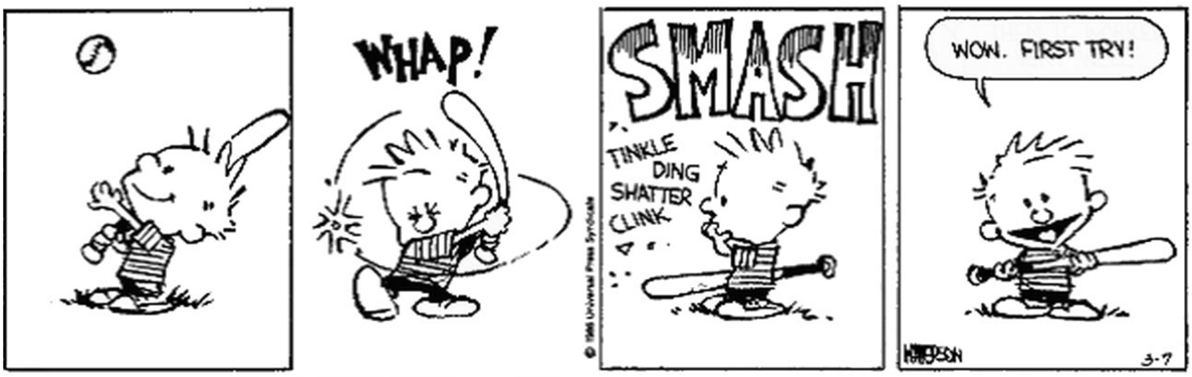
To clarify the different movement types, Schmidt & Lee (2005) proposed a continuum of movement types. On one end of the continuum are discrete movements, which have a clear start and end-point and are easily performed. At the other end of the continuum are continuous movements, which have neither a beginning nor an end, they can be performed continuously. Finally, in between are discontinuous movements, which can be seen as several discrete movements strung together. I suggest that the different movements show different effects because the planning and timing components vary. Easy and straightforward movements such as discrete movements are planned using feed-forward components, whereas movements that are more complex rely more on feedback loops. For example, the plan of a discontinuous movement might occur from one stop position to the next, since the movement is a connection of several successive discrete movements. The time in-between the movement (e.g. stops) allows planning of the next part of the movement trajectory as well as a recalibration of the new position. Thus planning of the second movement part might occur after the first is completed. Contrasting, continuous movements are most likely planned as a whole (Zelaznik & Lantero, 1996) and only are updated during movement execution.

The current experiments also investigate the flexibility of the human system. Without flexibility, we would be utterly stuck in specific and limited movement patterns. Being able to generalize or transfer learned information from a variety of tasks allows us to perform a far greater range of movements than those we ‘actually’ learned. The cost and energy to modulate a similar behavior to fit a slightly changed environment is far smaller than for re-learning an entire movement.

In the following chapter, I will first give a more detailed overview of the theories and mechanisms involved in visuomotor transformations and motor control. In the chapters thereafter, I will describe one experiment per chapter evaluating human drawing performance on lines and geometrical shapes while performing under a rotated visual feedback frame. The aim is to discover how we adapt to a rotation distortion, while performing different movement types. In addition, I hoped to learn how well or how much of the learned knowledge can be transferred, between movement types and between limbs e.g. arms.

CHAPTER 1

General Introduction: from Vision to Action



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From Vision to Action

Seeing an object and grasping it involves both visual and motor areas in the brain. On the one hand, the act of grasping an object involves several specialized visuomotor mechanisms such as estimating the size, orientation and shape of the object. Subsequently, object position in space must be encoded, transformed to allow for positioning of the eyes, hand, and prehension. In addition to these specialized mechanisms, there must also be coordination of all these mechanisms into a global action.

1.1 Classification of Motor Skills

Movement behaviors have been classified in various ways; there are two important classification schemes. The first, movement categories, is the discrete-discontinuous-continuous dimension based upon the particular movement made. The second, open versus closed dimension, is determined by the perceptual attributes of the task.

Movement Categories

Schmidt and Lee (1999, 2005) proposed a classification of motor skills based upon the movement kinematics used during a movement; they defined discrete, discontinuous and continuous motor skills. Discrete movements are movements with a recognizable beginning and end, such as kicking a ball or striking a match. Discrete movements are very rapid and (often) take only a fraction of a second to complete. Continuous movements represent the other end of the continuum. They have no identifiable beginning or end, the movement continues until stopped arbitrarily. Examples are swimming, running and steering a car. The final movement skill is neither discrete nor continuous, but rather incorporates features of both classes. Discontinuous or serial movements are best described as a number of discrete tasks strung together, which make up the ‘whole’ of the movement, such as starting a car.

In the current experiments, we tried to establish the same movement patterns using simple motions and geometric shapes. As a discrete movement task, we used center-out movements, which start in the center of the screen and move outward towards a marked position several centimeters away. For the discrete or serial task, we used a variety of geometric shapes, such as a triangle, a square, a hexagon and an octagon. Each shape exists of simple point-to-point movements strung together into a slightly more complex shape. The more ‘sub-movements’ a shape has, the more the complexity of the shape increases and the less familiar we are with the movement, for example the hexagon and octagon. In addition, to becoming more complex discontinuous movements with more angles also become more continuous because the angles become more obtuse (blunt). If we would increase the number of point-to-point movements to say, one-hundred we would have a circle. A circle would represent the last movement task, continuous movements. In the current study, the continuous tasks used a circle and a continuous star-shaped form. The latter shape was designed in such a way that it incorporated changes of direction which could be made without stopping or pausing the movement, as is the case with discontinuous movements (because of the acute angles). In the end we believe we created a rather well designed continuum of different shapes representing each of the three classes described as well as a few overlapping ones.

Open versus Closed skills

Another rather important factor in the classification of movement skills is environmental predictability. ***Open skills*** are skills for which the environment is constantly changing so that the performer cannot effectively plan the entire movement. The measure of success in executing a motor behavior in such a changing environment lies within the successful adaptation of the skill to its changing environment. In contrast, ***closed skills*** occur in a variable but predictable environment, meaning that changes are predictable or learned through practice. This allows us to plan the movement in advance before we execute it. Of course, some skills are semi-predictable and can be classified somewhere between the ends of the open-closed continuum.

1.2 The Transformation between Vision and Action

There are three main components involved in the transformation from vision to action: planning, control and learning. ***Motor learning*** is the ability to learn a novel task or to repeat an old task in a novel environment. To be able to do this we need a component that allows us to observe and correct our movements with respect to the environment, i.e., ***motor control***. In addition, it should allow us to adjust the movement while being performed, so it needs to be a rather quick loop. Finally, we manage to plan the movement in such a way that the error reduces itself as we learn the movement, i.e. motor planning and motor learning. Now we can remember the task so that in case we are required to perform this task again, we can rely on a learned basic motor plan, executing the movement as accurately as possible. Each of the ‘movement levels’ intricately linked to each other brings with it its own specified questions as well as overall questions concerning movement. In the following sections, I will discuss each component separately.

1.2.1 Movement Planning

The first and foremost problem is a question that has intrigued scientists for years. How do we combine visual information of the position of the target and limb with proprioceptive information to produce a correct motor command? These transformations from the visuomotor system to produce a grasping movement imply simultaneous control of several visual and motor mechanisms. The visual system needs to encode the object's characteristics, its size and orientation. The motor system needs a position encoding of distance and direction in reference to head, body and arm position. Furthermore, it needs a motor plan and a way of controlling the execution of this plan. One option would be to transform the desired sensory consequence into a motor command that would achieve the sensory consequence (Wolpert, Ghahramani & Flanagan, 2001). In this case, we would transform the extrinsic perception into an intrinsic movement plan. The alternative would map the motor commands onto their sensory consequences, meaning we transform our intrinsic movement plan to the extrinsic perception. These two options form the basis of two main views, which have established themselves throughout the years.

The first view, ***Equilibrium Point Hypothesis (EPH)***, proposes that the visual scene encodes extrinsic coordinates into a set of arm orientations or joint coordinates, i.e. an extrinsic to intrinsic transformation. Meaning that before the movement starts, our brain figures out where our arm needs to be, i.e., its desired end position. It then selects a path of how to reach this position, and transforms this path into a pattern of joint co-variations, so-called equilibrium points, which guide our arm to the desired end position. Subsequently, the brain defines the arm orientations from the initial position to the final position, movements are represented as intended final limb positions and as smooth transitions between these stable equilibrium points. The muscles follow a spring-mass system with a variable length-tension relationship, pulling joints into their equilibrium positions, corresponding to the final limb positions (Feldman, 1986; Bizzi, Hogan, Mussa-Ivaldi & Giszter, 1992; Flanagan, Ostry & Feldman, 1993; Shadmehr, 1998). Generally, the equilibrium point hypothesis associates movements, especially fast movements, with a higher muscle stiffness to counteract unwanted rotational forces (Flash, 1987; Flanagan et al., 1993; Gomi & Kawato, 1996; Spencer & Thelen, 1999). However, muscle stiffness is not always constant and extremely hard to measure (Gomi & Kawato, 1997; Osu, Uno, Koike & Kawato, 1997). Another assumption, based on the mass-spring properties of muscles, is that unexpected external perturbations should not affect a movement's final accuracy. However, asking subjects to perform movements in a rotating room showed that transient perturbations did influence a movement's final accuracy (Lackner & Dizio, 1994; Dizio & Lackner, 1995). Moreover, since EPH states that movement positions are determined as intended final positions, changing the workspace location should influence the hand trajectory. Morasso (1981) showed that hand trajectories remained roughly invariant when initial and final positions changed (see Gordon, Ghilardi & Ghez, 1994; Kriticos, Jackson & Jackson, 1998). A study by Baraduc & Wolpert (2002) showed that learning a visuomotor distortion was posture-specific and thus could not be the result of learning different postures; they proposed that this generalization was due to a translation into a Cartesian endpoint trajectory.

The second view, ***Vector-Coding Hypothesis (VCH)***, argues the exact opposite of the EPH. Namely, that the brain transforms an intrinsic pattern of joint co-variations into an extrinsic plan along a direction and distance vector (Morasso, 1981; Abend, Bizzi & Morasso, 1982; Hollerbach & Flash, 1982; Flash & Hogan, 1985; Gordon et al., 1994; Wolpert, Ghahramani & Jordan, 1995a; 1995b; Ghilardi, Gordon & Ghez, 1995; Haggard, Hutchinson & Stein, 1995; Krakauer, Ghilardi & Ghez, 1999; Prager & Contreras-Vidal, 2003; Vindras & Viviani, 2002). A translation into Cartesian (extrinsic) coordinates means we plan a movement along a specific direction and monitor our movement to keep it on the right path to reach the desired target location. If necessary, we will correct the movement path using visual feedback from our environment. According to the vector hypothesis, contrasting EPH, initial starting positions transfer across workspace as long as directions are similar (Wang & Sainburg, 2005). Moreover, the vector-coding hypothesis does not need the assumption of muscle stiffness to allow trajectory planning and generalizations across workspace (Gomi & Kawato, 1996; 1997).

A main part of the discussion in movement planning still evolves around whether we code space as intrinsic or extrinsic space. This question has not yet been resolved since compelling evidence for either view exists. However, when trying to fill the gaps of knowledge other questions appeared. For example, the question rose whether movement extent and direction are modular or interdependent, meaning coded independently from each other. Kurtzer, Herter & Scott (2005) found specialized neurons for control processes underlying movement and posture, leading them to believe that processes for movement and posture are modular. Ghahramani and Wolpert (1997) showed that participants could simultaneously learn two starting-point dependent visuomotor mappings, hereby proposing that the visuomotor transformation process is modular. Krakauer and colleagues (1999; 2000) demonstrated categorical differences in the time course and generalization of adaptation to induced errors in movement extent and direction, suggesting that the brain processes errors in extent and direction separately (Bock & Arnold, 1992; Prager & Contreras-Vidal, 2003). On top of these main and relevant questions about motor planning there are also many questions related to motor control, that is how we control a movement when executed, how we learn adaptations to distortions, how we change or update the planned movement using motor or visual feedback.

1.2.2 Movement Control

As previously mentioned, movement behaviors have been classified in various ways. Motor control concerns itself with the attributes of the task related to open- or closed-loop control.

Open-loop and Closed-loop control systems

Closed-loop control systems heavily rely on the concept that we use sensory or afferent information to regulate our movements. This can be information about the environment, our body state or the state of our body in relation to the environment. The closed-loop system has a specific goal, which is the input for the reference mechanism. This reference mechanism compares the goal to a sample obtained from the environment and computes an error. This error is given to an executive level, which instructs the effector level in how to reduce this error. The effector is the actual output of the system, which reduces the error. When the error reaches zero the executive level shuts off. The system is closed-loop because it goes from environment to decision to action and back to environment again (Schmidt & Lee, 2005).

In contrast, the open-loop control system does not rely on sensory mechanism, as does the closed-loop system. The open-loop system has an executive ‘programmed’ with instructions, which are sent to the effector from time to time, and the effector carries them out without the possibility of modification (Schmidt & Lee, 2005). The earliest open-loop system, the ***response-chaining hypothesis***, as described by William James (1890), who assumed that a movement began with a muscular contraction caused by an external or an internal signal. In turn, this contraction generated sensory information (feedback) from the muscles and/or produced movements, which served as another trigger for the next contraction. The difference to closed-loop control is that the feedback does not influence the movement. The open-loop system does not compare its input to any prior state. The input mainly serves as a trigger for the next act in a sequence. The actions of such a model can be influenced by the delay or degradation of the sensory information.

Visual Control of Movements

In light of the two control systems described above, vision is most certainly the most critical receptor for supplying information about movements, objects and movements of object in the environment. The concept of a dual visual system, one part processing information about feature and shape allowing identification of an object and the other providing information about the location of the object in visual space (Schneider 1969; Trevarthen, 1968; Ungerleider & Mishkin, 1982), led to the formulation of the visuomotor channel hypothesis. Paillard (1982; review in Paillard, 1996) suggested a model of how visual information influences the control of reaching and grasping movements. It divides visual information into three separate channels. (1) An 'identification channel' for selecting and steering specific motor pathways that orient and shape the hand grip in accordance with the size, form, and orientation of the object to be efficiently grasped. (2) A 'localization channel' that triggers the motor program of reaching in the right direction and extending according to the target localization. (3) An 'adjustment channel' to feed the corrective feedback loop that guide the directional transport of the hand and its smooth homing in on the target with the fine visual adjustment of the grasping.

The influence of two separate forms of visual information, namely static and dynamic, on motor control has been widely accepted. The first source corresponds to the 'classical feedback' based on the detection of the positional error signal between hand and target, whereas the second is based on the presumed detection of a directional error signal between the on-going movement trajectory and the gaze axis. The basic assumption is that positional and directional corrective feedback signals derive from two different visual input modes depending on retinal eccentricity (reviewed in Paillard, Jordan & Brouchon., 1981; Paillard & Amblard, 1985; Bonnet, 1975, 1977, 1981). The common understanding is that we use motion information early during movement and position information for endpoint control (Paillard, 1982; 1991; 1996). A recent study by Saunders and Knill (2004) investigated the influence of motion and position information on feedback control during online movement using a rotation distortion. They concluded that both components are needed for online control but that both were equally fast and begun when the hand was near peak velocity. Another study found that during adaptation subjects did not attempt to correct the imposed directional errors via feedback during movements, i.e., use online control; rather they used visual feedback primarily to change the direction of subsequent movements (Krakauer et al., 2000).

Several studies throughout the years focused on these two kinds of feedback. Berthier and colleagues (1996) varied the amount of visual information available during reaching and grasping movements, they showed that when the amount of information was decreased subjects had longer movement times and lower movement speed. Moreover, their movement profiles became more asymmetric and they over-compensated grasp aperture and grip size. In general, studies on removal of visual feedback have led to contradictory results. Carlton (1981a, 1981b), for example, found vision of the hand to be critical in a reaching task, whereas Jakobson & Goodale (1991) did not find any changes in movement kinematics or movement time. Jeannerod (1984) showed that reaches with visual feedback had longer movement times than reaches without. He suggested that this effect might be due to additional visual processing taking more time. Studies investigating reaching with blindfolded subjects reported longer movement times and slower velocities (Chieffi & Gentilucci, 1993), whereas others found no differences in movement time between blindfolded and not blindfolded participants in reaching (Wing, Turton & Fraser, 1986). Studies investigating the use of feedback to correct movements show a lot of controversy. This makes it extremely hard to predict behavior on a reaching task and the influence of feedback.

Movement Control models

Despite or perhaps in spite of these contradictory results a large body of research focused on the question: how do we use visual feedback in movement? When wanting to reach for an object, we first focus the object on our fovea. Next, our brain develops a movement plan of how to reach the desired object, which arm to use and how to use it. Subsequently, activated arm muscles move our hand along the planned path. The eyes follow the movement, providing feedback by detecting deviations and if necessary guiding the hand back on its course. This day-to-day example describes several processes that researchers have tried to discern and elucidate for years. The question about the importance of visual information during hand movements has its origin in the observation that removing visual feedback from the beginning of a movement does not affect performance accuracy whereas preventing visual feedback during the end or approach phase of a movement greatly increased spatial errors (Woodworth, 1899; review in Jeannerod, 1988). Woodworth stated that movements are comprised of two components. The initial-impulse phase, i.e. the ballistic or programmed movement phase, sends an impulse to the hand driving the limb towards the target. Once the movement has started, there are opportunities to correct the movement path by using visual feedback, which is the control phase. However, this correction can only occur if there is sufficient time to process the visual information. Thus, researchers investigated the role of visual feedback in hand- and arm-movements and through the years formulated several theories.

When we talk about feedback, we refer to the principal mechanism mediating hand path corrections. These hand path corrections result from a comparison between estimated hand location, i.e., the assumed location after movement initiation, and the target position. Essentially, it allows modulation of the initial motor command when this is inaccurate. As soon as the system detects a deviation from the planned path, feedback is the mechanism that alerts us of this deviation. The type of feedback detecting the deviation can be one of three categories. First, there is ***sensory feedback***, which estimates hand location based on sensory information; this is afferent[1] information that leads to a perception. As a second type, ***non-sensory feedback*** uses efferent[2] information to estimate hand location. Finally, there is ***internal feedback***, where the hand location is estimated using both efferent and afferent information. Feedback in itself refers to any of these categories. Based upon the feedback categories a burst of research started, trying to discern the feedback mechanisms used in hand and arm movements. This in turn led to the postulation of three types of models; feed-forward, feed-backward and hybrid models.

The ***feed-forward model*** posits that a motor command is defined before movement onset, and that sensory feedback loops are too slow to contribute to trajectory control. The role of feedback in movement control is trivial and restricted to the very end of the trajectory, when hand velocity is low (Keele, 1968; 1981; Arbib, 1981; Meyer, Abrams, Kornblum, Wright & Smith, 1988; Milner, 1992; Plamondon & Alimi, 1997). The second type of model is the ***feedback model***, which proposes that there is no a priori motor plan but rather a real time comparison between hand and target location (Hinton, 1984; Flanagan et al., 1993). Finally, ***hybrid models*** combine both the feed-forward and feed-backward hypotheses. Before movement onset, a basic motor plan is developed, but this is continuously monitored by internal feedback loops to allow online corrections of the movement (Pélisson, Prablanc, Goodale & Jeannerod, 1986; Prablanc & Martin, 1992; Hoff & Arbib, 1993; Desmurget, Epstein, Turner, Prablanc, Alexander & Grafton, 1999). The suggested neural structure that

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[1] In the nervous system, afferent neurons, otherwise known as sensory or receptor neurons carry nerve impulses from receptors or sense organs toward the central nervous system. Information is sent from arms, hands, legs, etc to the Central Nervous System.

[2] In the nervous system, efferent nerves, otherwise known as motor or effector neurons, carry nerve impulses away from the central nervous system to effectors such as muscles or glands. Information sent from the Central Nervous System to the periphery, e.g. arms, hands, legs, etc.

can implement these models is the cerebellum. A large body of research investigated the precise role of the cerebellum in feedback mechanisms. Miall, Weir, Wolpert & Stein (1993) suggested that the cerebellum uses a ***forward model***, providing rapid predictions of the motor commands, as well as a second model of time lags, which delays the predicted sensory feedback so a direct comparison with the actual sensory feedback is possible. Contrasting, Kawato & Gomi (1992) suggested an ***inverse model***, which translates information about the desired trajectory into the required motor commands.

Of these three models, the feed-forward model has received the most support over the last years. Three lines of results underlined the dominating position of the feed-forward model. First, deafferentation[3] studies showed that removing every sense of proprioception[4] did not prevent subjects from performing relatively accurately (Jeannerod, 1988; Taub, Goldberg, & Taub, 1975; Bard, Turrell, Fleury, Teasdale, Lamarre & Martin, 1999). Other studies showed that visual feedback loops are too slow (e.g. 190-260 ms) to allow efficient trajectory control at the initial phase of the movement (Keele & Posner, 1968; Elliott & Allard, 1985; Bhavin & Shimojo, 2002). Based on these results, they concluded that sensory feedback loops could not be used to control hand trajectories. However, other studies provided the contrasting results that deprivation of proprioception did lead to dramatic motor impairments (Jeannerod, 1988; Rothwell, Traub, Day, Obeso, Thomas & Marsden, 1982; Sainburg, Poizner & Ghez., 1993). In addition, related studies found that goal-directed movements were more accurate when proprioceptive or visual information was available (Keele, 1981; Arbib, 1981; Meyer et al., 1988; Milner, 1992; Plamondon, & Alimi, 1997, Bédard & Proteau, 2003). Finally, Adams (1977) and Abbs, Gracco & Cole (1984) provided evidence that proprioceptive feedback loops take less time than visual feedback loops.

These results led to the forming of a fourth model, the ***dual model of motor control*** incorporating the findings that accuracy improves when visual and proprioceptive information is present (review in Desmurget & Grafton, 2000). It was then suggested that there are two main components contributing to the control of hand and arm movements in reaching. The first is a fast initial phase that is primarily ballistic and concerns the positional error between hand and target, whereas the second slower adjustment phase concerns the information about

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[3] Deafferentation is the elimination or interruption of sensory nerve impulses by destroying or injuring the sensory nerve fibers. The afferent connection with the central nervous system is incomplete or the dorsal roots are transected (for medical purposes). Dorsal roots carry only sensory axons innervating the limbs, thus motor innervations of the muscles remain intact, but sensory information is lost.

[4] Proprioception is the sense of static positions and movements of the limbs and body.

the motion of the hand based on the directional error signal between the on-going movement trajectory and the gaze or end-point (Paillard, 1996). The latter is thought to be under guidance of sensory feedback (Jeannerod, 1988), which is mainly used early during movement, whereas position information is used for endpoint control (Paillard, 1996). Desmurget and colleagues (1999) observed a loss of accuracy when online feedback loops were disrupted supporting that position information is used for endpoint control.

A recent study, however, provided contrasting results. Saunders & Knill (2004) showed that during online control motion and position information were both necessary, they were equally fast and both began when the hand was near peak velocity. Other studies showed that removing vision of the hand completely affected both accuracy and movement kinematics (Jakobson & Goodale, 1991). The variability in endpoint accuracy greatly increased (Keele & Posner, 1968; Carlton, 1981; Zelaznik, Hawkins & Kisselburgh, 1983; Beaubaton & Hay, 1986) as well as the curvature of the reaching paths (Sergio & Scott, 1998; Goodbody & Wolpert, 1999). Furthermore, longer movement times became apparent, as well as the tendency to undershoot target distance (Prablanc, Echallier, Jeannerod & Komilis, 1979; Jeannerod, 1984; Prablanc & Pélisson 1990; Berthier, Clifton, Gullapalli, McCall & Robin, 1996). Additionally, Jakobson and Goodale (1991) showed that when visual feedback and no visual feedback conditions were unpredictable subjects adopt a no visual feedback strategy, i.e. they did not use feedback on those trials were it was available to improve their pointing accuracy (Zelaznik, Hawkins & Kisselburgh, 1983; Elliott & Allard, 1985). The general assumption is that these effects result from a lack of information about the initial hand position for movement planning and/or visual feedback from the hand during the final movement phase (Baraduc & Wolpert, 2002). More specifically, changing the hand used or changing the location of the joystick in a blind pointing task dramatically disrupted performance, changing both was more disruptive than changing only one feature (Rosenbaum & Chaiken, 2001). Contradicting these findings, Wang & Sainburg (2005) showed that a rotation adaptation is stored or processed independent of body coordinates and initial arm positioning.

The variations used in visuomotor tasks are numerous, and as the studies mentioned above show findings are still contradictory depending on task demands, e.g. having a visual target or not, being able to see the moving limb, switching limbs, changing locations and more. In the current study, we present a visuomotor experiment where participants were not able to see the moving limb but where a cursor position on the screen was available representing hand movements. The absence of visual information about position of the moving limb should not interfere with correction of the trajectory of movements (Péllison, Prablanc, Goodale & Jeannerod, 1986; Prablanc, Pélisson & Goodale, 1986).

1.2.3 Movement Transfer or Generalization

Motor studies are often interested in how much 'knowledge' is transferred from one task to another, because being able to adapt to new situations is essential for humans in everyday life. This turns the question of transfer into a question of generalization. If we adapt to a dynamic or kinematic distortion in a certain task, can we generalize it to a different task, different limbs or even to a different workspace, or is the learned adaptation only reliable in a similar task and under similar circumstances? A large body of studies investigated generalization of kinematic and dynamic adaptations across distortions, workspace, and movement categories. Subjects trained on a gain distortion generalized the learned adaptation over distance, direction and workspace (Krakauer et al., 2000), whereas a rotation distortion task could be generalized over distance and direction, but only when a minimum number of 8 directions were trained could the rotation be generalized 100% to untrained directions (Bock, 1992; Krakauer et al., 2000; Wang & Sainburg, 2005). Tong and Flanagan (2003) showed a lack of interference on a kinematic rotation task for center-out versus figure eight drawing movements, when rotations switched between +30° and –30°. Using force fields revealed generalization across workspace (Shadmehr & Mussa-Ivaldi, 1994; Thoroughman & Shadmehr, 2000) as well as to other movement tasks such as center-out movements to circular movements (Conditt, Gandolfo & Mussa-Ivaldi, 1997). Abeele and Bock (2003) posed a relatively new plan, they investigated transfer across pointing and tracking, and they trained subjects on a pointing or a tracking rotation task and tested them on the untrained task. Their results showed that adaptation transferred substantially across movement categories and more from the pointing to the tracking task than in the opposite direction. This finding provided evidence that a rotation adaptation is stored/processed independent of body coordinates and initial arm positioning (Wang & Sainburg, 2005), clearly contradicting the results found by Baraduc and Wolpert (2002), which showed that initial arm positioning mattered for learning direction generalizations. Rosenbaum and Chaiken (2001) found results similar to Baraduc and Wolpert; they tested participants, where changing the hand used or changing the location of the joystick in a blind positioning task dramatically disrupted performance. Even more interesting, changing both hand used and location was more disruptive than changing only one feature. Intuitively we realize and know that if we performed or learned a certain action with one hand it would be rather difficult to perform it with the other (untrained) hand.

However, researchers are always interested in studying how much of the learned information is transferred to the other hand or even another limb.

Handedness and movement skills

The medial longitudinal fissure separates the human brain into two distinct cerebral hemispheres. The two sides of the brain are similar in appearance, and every structure in each hemisphere is mirrored on the other side, yet despite these strong similarities, the functions of each hemisphere are different. Lateralization of brain functions is for example evident in the phenomena of right- or left-handedness. The definition of handedness is the unequal distribution of fine motor skills, such as hand-eye coordination, between the right and left hand. Right-handed people are generally more skilled with the right hand whereas left-handed people are more skilled with the left hand. Commonly, people are right-handed, only 8 to 15% are left-handed (Hardyck & Petrinovich, 1977).

Theories of handedness propose that handedness is more than a simple preference for one hand (Guiard, 1987; Kabbash, Buxton & Sellen, 1994), because hands work together in more subtle ways. For example, when writing on a piece of paper, it is not a simple matter of one hand being dominant and writing on the paper. For a right-handed person, the left hand is involved in important ways: it orients the paper and provides the context from which the right hand operates. Naturally, this is similar for left-handed people. Interestingly, studies investigating handedness found profound performance differences on a large scale of tests between left- and right-handed participants.

A related question, the matter of transfer of learning received a large amount of attention. Transfer or interference of learning as defined by Schmidt and Lee (1999) refers to the effect of experience in a prior task on the performance of learning a novel task. More specifically, practice on one task causes a gain or loss in proficiency on a different task. Inter- or intra-limb transfer of learning relates to a change in proficiency on a motor task with a particular limb as the result of practice with a different or contralateral limb on the same motor task, without any prior involvement of the latter during task acquisition. Throughout the years, studies showed transfer effects of motor learning to different motor systems (Keele, Jennings, Jones, Caulton, & Cohen, 1995; Grafton, Hazeltine & Ivry, 1998; Kelso & Zanone, 2002). Most studies addressed transfer between dominant and non-dominant hand i.e. intermanual transfer (Imamizu & Shimojo, 1995; Thut, Cook, Regard, Leenders, Halsband et al., 1996; Thut, Halsband, Regard, Mayer, Leenders et al., 1997; Sathian & Zangaladze, 1998; Temprado & Swinnen, 2005). As a result, an interesting finding appeared, namely that intermanual transfer effects are not always symmetrical. In some cases intermanual transfer was better from dominant to non-dominant hand (Parker-Taillon & Kerr, 1989; Parlow & Dewey, 1991; Thut et al., 1996) in others transfer was better from non-dominant to the dominant hand (Parlow & Kinsbourne, 1990; Rosenbaum & Chaiken, 2001). Additionally, there are studies reporting intermanual symmetry, with transfer to the dominant hand being similar to transfer to the non-dominant hand (Piccirilli, Finali & Sciarma, 1989; Mandal, Singh, Asthana, & Srivastava, 1992; Rand, Hikosaka, Miyachi, Lu & Miyashita, 1998; Schulze, Lüders & Jäncke, 2002). As a side note, intermanual transfer effects seem to depend on handedness (Stoddard & Vaid, 1996) and gender (Schmidt, Oliveira, Rocha, & Abreu-Villaca, 2000), whereas other studies did not find these effects between right- and left-handed participants (Mandal et al., 1992; Yamauchi, Imanaka, Nakayama, & Nishizawa, 2004) or between males and females (Alvis, Ward, & Dodson, 1989; Parlow & Kinsbourne, 1990).

Here, we study intermanual effects on motor transfer from the dominant to the non-dominant hand on an adaptation task across different movement categories. Participants performed naïve and pre-adaptive baselines with both hands, but were adapted using either their right or left hand and thereafter tested with both hands again. We expected to find a positive transfer from dominant hand adaptation to non-dominant hand performance as shown in earlier studies concerning motor transfer.

1.3 Chapter Outline

Each of the following chapters describes a separate experiment. The aim of each experiment was to study the effect of a visuomotor rotation across different movement categories (discrete, discontinuous and continuous). Moreover, I wanted to study the effect and adaptation of the visuomotor rotation within each of these movement categories, as well as the generalization to the other movement categories. In each experiment, participants performed a drawing task using a stylus on a horizontal writing tablet. The drawing movements of the stylus were represented on a vertical screen in front of them, whereas their actual hand movements were hidden from sight by a non-transparent box.

In chapter 2, the first experiment investigated whether participants could perform and adapt a visuomotor rotation while performing discrete and discontinuous movements. The experiment consisted of two tasks; a line drawing/center-out task (discrete movements) and tracing of polygon shapes (discontinuous movements). The line drawing task used either 4 or 8 target positions and the polygon shapes were a triangle, square, hexagon and octagon. The idea was that discrete movements are planned as a whole prior to movement execution without much need for feedback. Under normal, i.e., undistorted circumstances, participants do not need to rely on feedback to draw a line between two points, because it is such an easy, well-known and well-trained movement. In contrast, a geometric shape such as a triangle, even though it is a well-known shape is more complex and probably relies more on feedback and on a more basic plan for the shape. Thus, we expect that under normal conditions participants will be able to perform both tasks equally well, even though each movement relies on a slightly different planning approach. However, as soon as the distortion is 'activated' and the visual information no longer corresponds with the performed movement, participants are 'forced' to rely on the presented feedback. Now the differences in pre-planning should become visible, and results showed they do. Relying only on the feed-forward plan of a movement (e.g. discrete movement) heavily disrupts the movement when the rotated feedback is presented, whereas a movement with less of a feed-forward plan (e.g. discontinuous movement) already relies on feedback, thus disrupting movements less. Eventually, with sufficient training, however, both movement categories show adaptation to the rotation distortion. The experiment showed a profound difference for the hexagon and octagon. Both were less affected by the rotation distortion than any of the other movements. Thus I speculated that the more complex or more continuous a shape the less of this feed-forward planning occurred before movement execution. Naturally, one should depend more on the feedback provided via the screen.

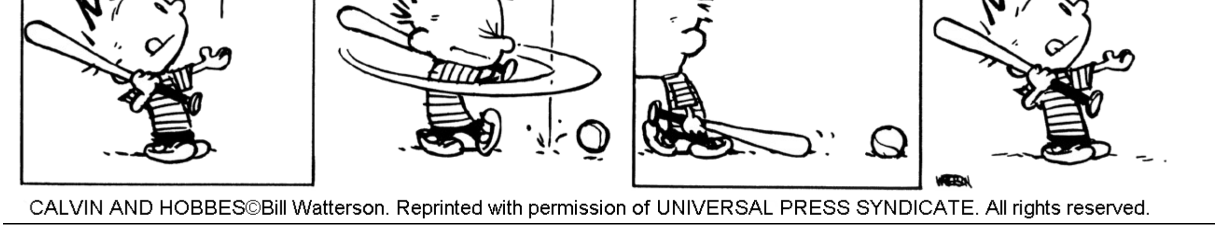
In chapter 3, I further explored the effect of a visuomotor rotation but now including continuous movements, thus testing discrete and continuous movements. A continuous movement such as a circle, which differs from the previously tested movements in that it, has no start- or end-position, no reference points or corners and no 'sudden' changes of direction. Therefore, I designed two further shapes, which were curved star shapes with either 4 or 8 curves (see pg. 40). These shapes were both continuous in their movement but included changes of direction. Participants again were tested under normal and distorted visual feedback conditions. The expectation was that the continuous shapes should show even less of an effect of the rotation distortion than the hexagon and octagon, because, the complexity of the shape allows for only a very basic movement plan and relies on continuous feedback during movement execution. The results did indeed show that the effect of the rotation distortion was far less than in any of the other movement categories.

In the next experiment described in chapter 4, I focused more on the internal representation of the movement plan. The first two experiments showed that if a movement plan was already fully developed before movement onset, the distortion on the visual feedback led to increased errors in performance. The results showed that the more complex a movement (e.g. continuous movements) the more we rely on the visual feedback presented. In theories of visual guidance, commonly describe the mechanism of visual feedback as an 'error detection mechanism'. The motor system notices a deviation from the actual movement and the expected or planned movement towards the target. It then tries to minimize this error and continuously check the deviation error. Hence, I was interested in what would occur if the reference i.e. the target location or shape was removed. To test this, I only used discrete and continuous movements, but instead of showing the target continuously, it was removed after a brief period (before movement onset). Now participants could only rely on the internal plan and partially on their movement feedback, but since the latter could not be connected to a specific target, the 'error detection mechanism' should be relatively abundant. Therefore, I expected fewer errors when no visual target was present. The results showed that the unavailability of the target only mattered in case of the continuous movement. The last three chapters describe the effects of a visuomotor rotation across different movement categories. Within each chapter a more detailed view is given, also incorporating the generalization to other movement categories. The next and final chapter moves on to the question concerning generalization across limbs or effectors.

In the final chapter, I investigated the effect of a visuomotor rotation on intermanual transfer across movement categories. The task consisted of a selection of movements from each movement category: 4-point and 8-point (discrete), square and octagon (discontinuous) and 4-curved and 8-curved shapes (continuous). Subjects trained a specific trial-type with either the right or the left hand and were tested on all other trial-types with the untrained hand. Based on previous studies we expected to find a positive transfer from dominant hand performance to non-dominant hand performance.

CHAPTER 2

Adaptation of Discrete and Discontinuous Movements



2.1 Introduction

One of the most controversial topics in motor control and motor learning is how we learn and plan movements. When we want to reach for an object or target, our brain has to process information of the visual target, the visual surroundings, where we are, relation of body parts to target and surroundings and it has to compute the most efficient way of reaching and grabbing the object. Considering all factors this is not an easy task. Substantial research has been done to discover how we plan arm movements and how we control them (using visual feedback). The current study will focus on the mechanisms involved in eye-hand coordination, such as planning control of arm movements and more specifically how well we can flexibly adapt the movement when faced with a rotation distortion.

A typical task used to study planning and control of arm movements is the so-called adaptation task. The task confronts a person with a relatively easy task, where they have to move or point towards a target in space. Since we are all experts at simple pointing, experimenters came up with ideas of distorting what we see or do. They did this in a large variety of ways; some distorted visual feedback by using prisms (Stratton, 1897a, 1897b; Ingram, van Donkelaar, Cole, Vercher, Gauthier & Miall, 2000; Jakobson & Goodale, 1989), rotations and gainfields (Bock, 1992; Abeele & Bock, 2003; Rosenbaum & Chaiken, 2001; Krakauer et al., 2000; Baraduc & Wolpert, 2002; Saunders & Knill, 2004; Wang & Sainburg, 2005). Others removed vision of the arm altogether (Péllison, Prablanc, Gooddale & Jeannerod, 1986), or induced a dynamic force field, which moved the arm in a different direction (Shadmehr & Mussa-Ivaldi, 1994; Thoroughman & Shadmehr, 2000). The variety of adaptation tasks is enormous, and as the large amount of studies show, we are quite capable of adapting to the 'new' task dynamics or kinematics in a relatively short time, revealing the flexibility of the human visuomotor system.

The question asked in all these studies was whether we learn movements in an intrinsic or extrinsic coordinate system. Extrinsic space can be defined in Cartesian coordinates; it locates points within a framework external to the holder of the representation and independent of his or her position, whereas in intrinsic space locations are represented with respect to the particular perspective of the perceiver (Klatzky, 1998, see chapter 1.2.1, pg. 4). These two coordinate systems match with two main theories ***Equilibrium Point Hypothesis*** (EPH) and ***Vector Coding Hypothesis*** (VCH). EPH assumes that we see objects in extrinsic (Cartesian) coordinates, and thus to be able to reach for an object in space we will have to translate the extrinsic coordinates into body (intrinsic) coordinates, by defining the positions the arm should move through to reach the object. In contrast, VCH states that we perceive space in intrinsic coordinates and have to adjust our movements to the ‘actual’ extrinsic space, by defining a direction and distance vector to the object. Both theories make several assumptions, the most important for EPH being the start position: if after adapting to a certain task the start position changes the newly learned knowledge is disrupted by changing the intrinsic coordinate system. In contrast, the VCH accounts for changing start positions without having to change the movement plan, hence it allows generalization to untrained directions (Krakauer et al., 2000). For example, if adapted to an upwards movement with a rotation distortion, EPH would predict difficulties when the tested movement is downward, whereas VCH states that the motor plan can generalize the learned distortion to untrained directions.

To my knowledge, few studies investigated adaptation across movement categories. Abeele and Bock (2003) compared 3D pointing and tracking movements under a visual rotation. Their findings showed more generalization from pointing to tracking than in the opposite direction. The current study was inspired by this study, although the current study uses tracing and drawing movements instead of tracking movements. Moreover, drawing and tracing are movements performed in a 2-dimensional space whereas pointing and tracking occur in a 3-dimensional space. Thus, the current results rely more on eye-hand coordination and feedback mechanisms.

The current study investigated how a rotation distortion influenced drawing (2D) performance across different movement categories. For this purpose, participants performed movements in two different movement categories as defined by Schmidt & Lee (2005; also see § 1.1, pg. 2): (1) discrete movements with a clearly defined start and end-point as when drawing a straight line, and (2) discontinuous movements which consist of 3 or more connected discrete movements as when drawing a triangle or square. The main hypothesis was that discrete movements are planned as a whole prior to movement execution without much need for feedback, thus only needing feed-forward components, whereas complex movements such as the discontinuous movements rely on a more basic feed-forward motor plan but also rely on feedback components to correct the movement during execution. We expect to find that the fewer feed-forward components are needed or used for the movement, the lower the influence of the rotation distortion will be. Participants will already rely more and more on the visual information provided and will adjust their movement plan quicker. Performing movements in two categories while training (adapting) in only one, allowed for a direct comparison of performance across movement categories. For example, if a participant trained on the 4-point trial in the discrete category and showed better performance on the triangle tracing after training, then this increase in performance was due to learning while training on the 4-point trial. Krakauer and colleagues (2000) showed that participants trained on a minimum of eight directions were able to generalize a rotation distortion more completely too untrained directions (see Bock, 1992; Wang & Sainburg, 2005). To be able to replicate these findings the discrete movement category consisted of two trial-types: a 4-point trial and an 8-point trial, using either 4 or 8 target positions aligned in a circular fashion at equidistant intervals. The expectation was that participants trained on the 8-point trial-type should show a better adaptation to the rotation distortion than participants trained on the 4-point trial-type. Moreover, I expected that the more complex the movement the better one eventually incorporated the distortion, thus being able to generalize it more easily to other untrained directions, e.g., from triangle to square as well as to other movement categories, e.g., from discontinuous to discrete movements.

2.2 Methods

Subjects

Sixty-six right-handed students of the Ruhr University Bochum participated in the study. Each condition: 4-points, 8-points, triangle, square, hexagon, and octagon, had an equal number of participants. All participants were naïve as to the purpose of our study and had no motor deficits. The experimenter explained the task and setup before participants signed an informed consent, which the local Ethics Committee approved. Participants received a fee of 10 euro for participation.

Material and Apparatus

Participants sat at a desk, facing a (vertical) computer screen and a (horizontal) WACOM writing tablet in front of them. The tablet was placed underneath a cover-box, which hid the tablet from sight but allowed hand movements underneath. The computer screen for stimulus presentation was placed on top of the cover-box. This setup allowed participants to see the task presented on the screen. While participants moved across the tablet, they were not able to see their actual hand movements. Instead, a continuous black line visualized on the screen represented their hand movements. Participants had to rely solely on this feedback to control their hand movements. The program for creating the stimuli and recording the data was written using MATLAB using the psychophysics toolbox (Brainard, 1997; Pelli, 1997).

The program presented a list of different trial-type possibilities, of which the experimenter could pick the desired trial-types used during the experiment. Depending on these choices, the program created and presented target dots and/or several shapes on the screen. Participants performed the task on a WACOM writing tablet using a wireless stylus, which was held like a regular pen. The participants' movements, recorded throughout each trial, were the x- and y-coordinates of the pen while the pen was on the tablet. Error measurements based on the pen-data were calculated using MATLAB.

Task and Procedure

The experiment used six conditions defined by the specific trial-types categorized in two movement categories: (1) center-out point-trials, requiring discrete center-out movements and (2) polygon shape trials, requiring discontinuous movements. The center-out point-trials consisted of either 4 or 8 points distributed at regular equidistant intervals in a circular fashion (see Figure 2.1; Top). Participants were required to move from the center cross to one of the 4 or 8 points displayed on the screen. The polygon shape trials consisted of four different shapes with a certain number of corners, e.g. triangle, square, hexagon or an octagon (see Figure 2.1; Bottom). Participants started the movement at the start cross and traced the shape clockwise.

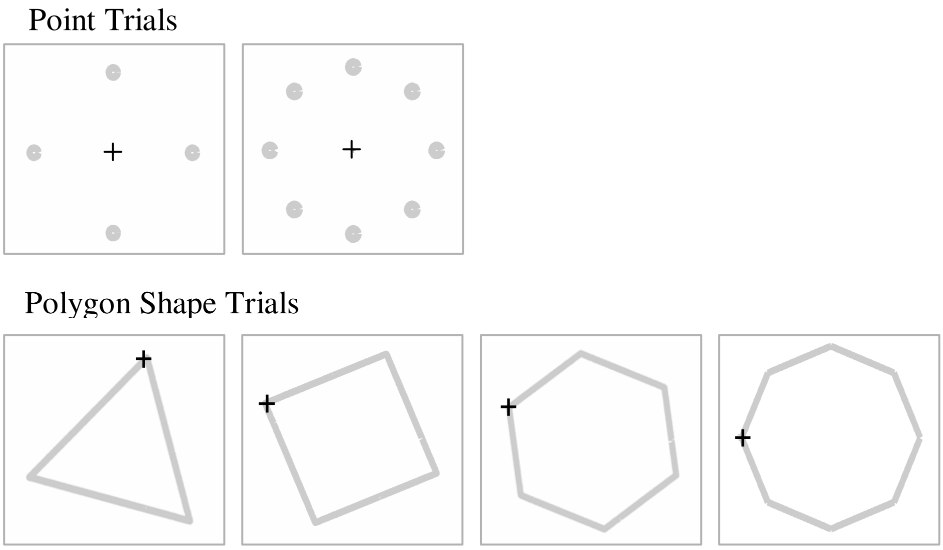


Figure 2.1 Center-out point trials and polygon tracing trials; Top;4-points trial and 8-points trial. Bottom; polygon shape trials, triangle, square, hexagon and octagon.

Participants first received a small example acquainting them with the pen and tablet, followed by a brief instruction. At the beginning of each trial participants saw a black cross, positioned either in the center of the screen or on the corner of a figure (as shown in Figure 2.1).

Participants were instructed to first position the cursor in the center of the cross after which they heard a tone and the target dot or shape appeared. Participants were then required to move the stylus across the tablet towards the target dot or trace the shape in a clockwise fashion. After reaching, the target participants had to push a small button using their index finger. The button was slightly above the grip position of the index finger. Upon the button press the screen was cleared and the start cross reappeared, indicating the next trial start. Note that to complete a 4-point trial the participant had to complete 4 sub-trials, one for each target dot.

The experiment started with a baseline measurement, measuring participants' performance on all (six) trial-types, meaning that when participants moved the stylus on the tablet, they could immediately observe their movements on the computer screen visualized by a black line (as would be the case when writing on a piece of paper). This is the naïve baseline, participants performed movements without a distortion, which was followed by a pre-adapted baseline. The pre-adapted baseline was the initial exposure of the participant to a 45° counterclockwise rotation distortion[5] to the visual feedback. The trials itself were identical, and movements were still shown immediately but now the visualization on the screen (the black line) was rotated by 45°. Meaning that for example a participant moved the stylus straight to the right (3 o'clock), the visualization of their movement on the screen moved right and upward (between 1 and 2 o'clock). Participants had to learn by trial and error to correct their movements by rotation 45° clockwise, i.e. to move the stylus right and down to produce a straight right movement on the screen. The rotation distortion was not velocity-dependent and uniform across the screen. During both baselines, each trial-type was presented three times.

After baseline acquisition, participants received one trial-type as training to learn/adapt to the rotation distortion. For example, if we would select the 4-point trial as the adaptation condition then we would measure baseline performance on 4-point, 8-point, square and circle trial, but throughout the entire adaptation phase, participants would only receive the 4-point trial. Trial-types were counterbalanced between subjects throughout the experiment. To keep the amount of adaptation at a similar level the number of center-out movements during adaptation was set to a total of 200 for the pointing trials and 100 for the tracing trials. The time spent performing 200 center-out movements and performing 100 shapes was similar

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[5] Calculated as: $\alpha = \Phi/180*\pi$. The rotation angle α is determined by Φ, here 45°.

across participants. Finally, participants received each trial-type once more still using the same rotation distortion while adapted performance was measured.

Data Analysis

To establish a good measure of whether subjects adapted to the distortion I used several different error measurements. I recorded participants' movements throughout the experiment and analyzed the ***Initial Direction Error*** (IDE), ***Movement Directions, Root Mean Square Error*** (RMS) and ***Mean Velocity*** (VEL). The Initial Direction Error (IDE) was computed after movement onset at a radius of 15 pixels from the start position (to filter out positioning errors) as the angular difference between two vectors (representing components of adaptation before feedback influences). The first vector was the movement vector made by the subjects' using the stylus. The vector started in the center position and ended at the 15 pixels radius cut-off surrounding the center. The second was the vector from the center point to the target stimulus. The error measure was the angle between the actual and the subject vector in degrees. Additionally, ***movement directions*** were defined during this process. For the center-out point-trials, I defined movement directions in angles from the center cross in the four cardinal and four diagonal directions. The horizontal movement to the right was defined as 0° e.g. movement direction 1, continuing clockwise with 4 movement directions for the 4-point trial (at 90° intervals) and 8 movement directions for the 8-point trial (at 45° intervals). The movement directions for the polygon shapes were defined starting from the start cross to the next corner as movement direction 1 (again computed in degrees), continuing clockwise with movement directions from corner to corner. Finally, I computed the ***Percentage of Adaptation*** using the initial direction errors, allowing us to see how large the adaptation was for learning from naïve to adapted performance, corrected for the error increase after distortion onset. I computed the percentage adaptation using the equation ***(pre-adapted – adapted)/(pre-adapted – naive)*100***, a 100% adaptation indicates that performance before and after training was similar.

Second, Root Mean Square error (RMS) represented the accuracy with which participants performed the center-out or drawing movements (including feedback corrections). I defined reference points for each line and shape in 0.5 degrees steps. For each of these points the program measured the distance between the position of the stylus and the reference position. The errors were the square root of the radial distance between the actual and the reference position, which were averaged for all 0.5° intervals were averaged and squared resulting in the mean distance that a subject's trajectory diverged from the ideal trajectory. Furthermore, I measured Mean Velocity (VEL) during each movement. Mean velocity was measured dividing the length of the trajectory by the time needed to complete the trajectory.

Effects were statistically analyzed using repeated measures ANOVA[6] with levels of training and trial-types as within factors. The levels of training were naïve- and pre-adapted baselines, and adapted-test performance. Trial-types were the trial-types used in the current experiment e.g. 4-points, 8-points, triangle, square, hexagon, and octagon. Between factors consisted of condition, defined as the matching trial-types used during the adaptation training, as well as the direction of movement (in IDE analysis only). In addition, for easier comparison in the graphs across the different trial-types I averaged the number of trials for all trial-types to a total of 25. Post-hoc analysis used a Bonferonni correction ($\alpha = .05$).

2.3 Results

Figure 2.2 shows an example of the performance of a typical subject throughout the experiment. It shows the subjects performance on each trial-type during each of the three training levels: Naïve, Pre-adapted and Adapted performance. The data set of the single subject show the typical results, performance is quite good in all naïve trial-types, the green lines are very straight and closely follow the original (black) shapes. When faced with the 45° rotation for the first time (pre-adapted performance) performance changes drastically. The subject's lines were curvier and diverged further from the original shapes, especially in the two point trial-types. Remember that after pre-adaptation the subject trained one specific trial-type for an extensive time. In the current example, the subject trained the 4-point trial 50 times to adapt to the rotation (200 movements, 50 trials x 4 directions). The last column depicts the adapted performance after training. The lines are straighter than before training, albeit not as straight as in naïve training. Throughout the experiment, we closely observed each subject's performance and discarded subjects who showed no performance loss when first exposed to the 45° rotation.

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[6] ANOVA uses a test statistic called an F value, which is the ratio of the Model Mean Square to the Error Mean Square under the null hypothesis that all the population means are equal; H_o: $\mu_1 = \mu_g$. The F statistic follows an F-distribution with a numerator *p* degrees of freedom and denominator *n-p-1* degrees of freedom.
Notation is as follows: $F_{(p,\, n\text{-}p\text{-}1)}$ = F-value, p < p-value.

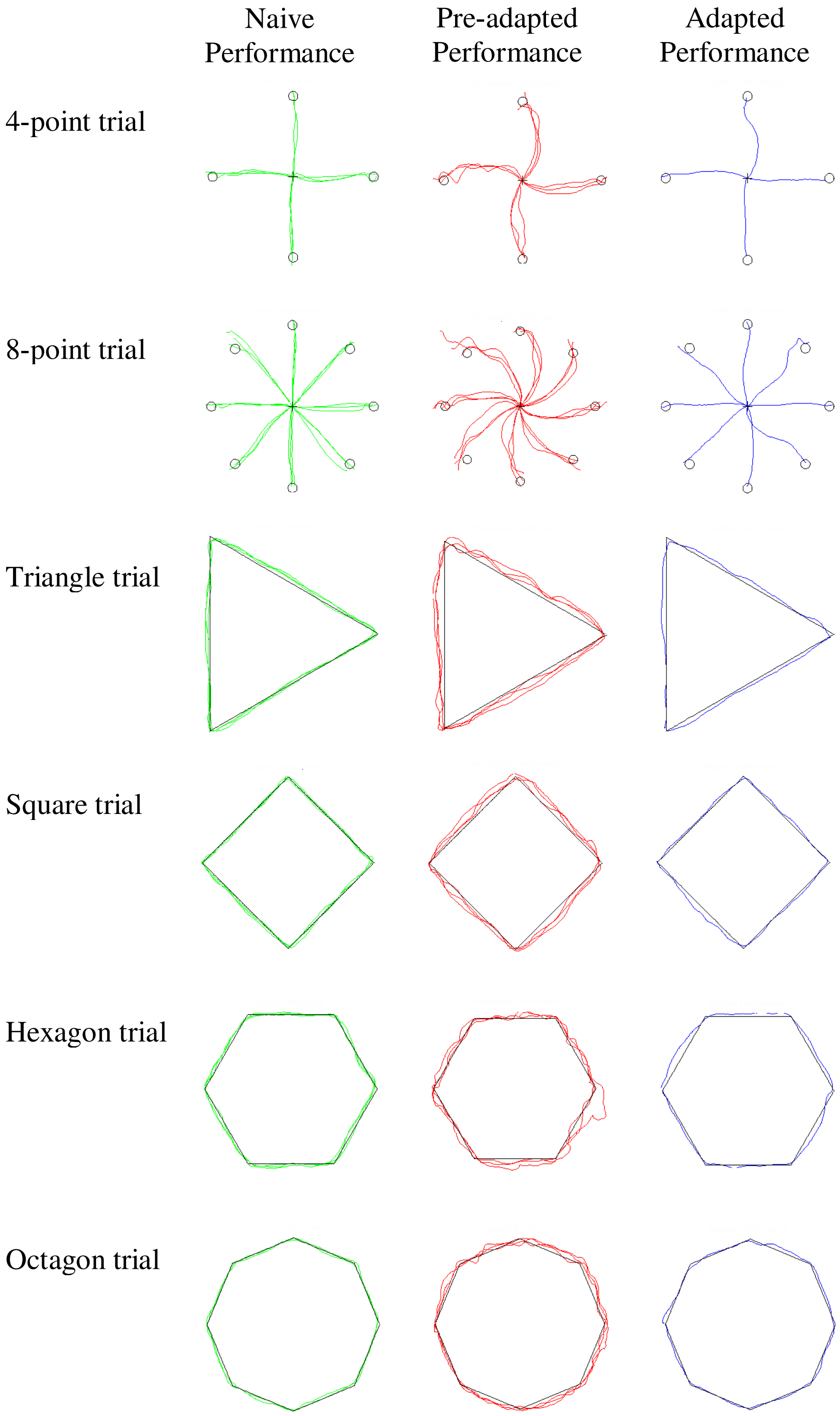

Figure 2.2 shows a full data set of a single subject for all trial-types for each level of training: Naïve performance (green, left column), Pre-adapted performance (red, center column) and Adapted performance (blue, right column). The black shapes represent the different targets.

2.3.1 Initial Direction Error

Figure 2.3 shows the time series adaptation for each trial-type (averaged across conditions) to evaluate overall differences. The first noticeable difference is that there is no large increase in direction error visible for both the hexagon and octagon trial-type. Further, as soon as the adaptation trials start direction errors are comparable for all trial-types and subjects ‘adapt’ rather quickly, participants only need around five trials to show minimal errors in direction.

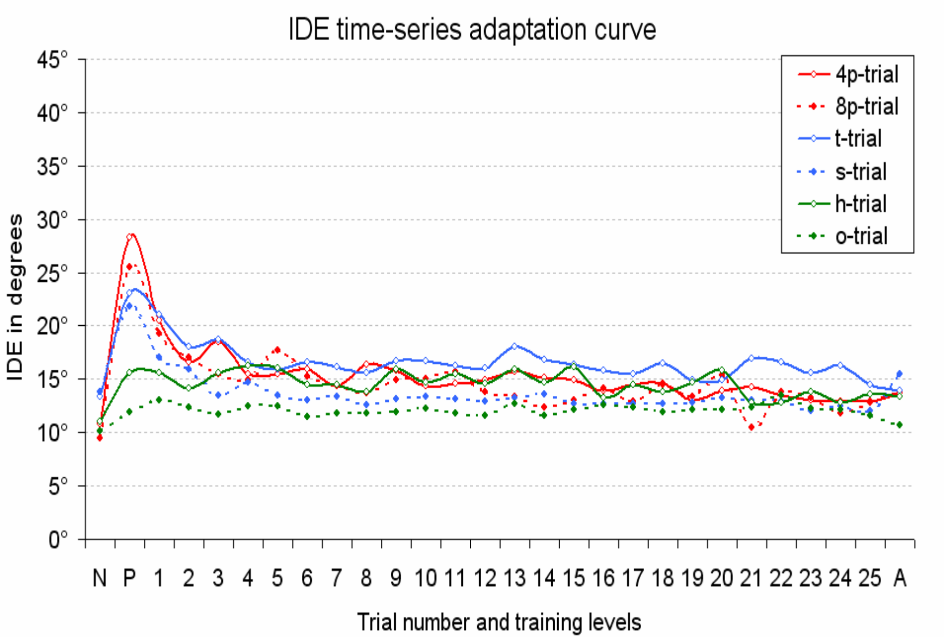

Figure 2.3 shows IDE time-series adaptation curve for all trial-types in relation to the rotation distortion (averaged across participants and conditions), N = naïve, P = Pre-adaptive baseline, training (matched for number of trials), A = Adapted-test.

Figure 2.4 shows participants’ pre-adapted performance (before training) plotted against adapted performance (after training) of each subject for all conditions on each trial-type. The lower half of the figure, labeled "Transfer", shows subjects who made larger direction errors during the pre-adapted trials than on the adapted trials, revealing that they adapted to the distortion to a certain degree. The upper part, labeled "No Transfer", shows the opposite performance with errors being larger after training than before. Participants in the 4-point and the 8-point conditions showed adapted performance for both point trial-types and the triangle and square trial-types. In contrast, they only showed minimal adaptation for the hexagon and octagon trial-types. The single subjects' and group averages (colored crosses with group standard deviations) are close to the centerline, representing errors of the same magnitude on both pre-adapted and adapted performance. Participants who trained on the polygon shape trials showed similar behavior on the 4-point, 8-point, triangle and square trial-types, whereas the hexagon and octagon trials-types only showed minimal adaptation again.

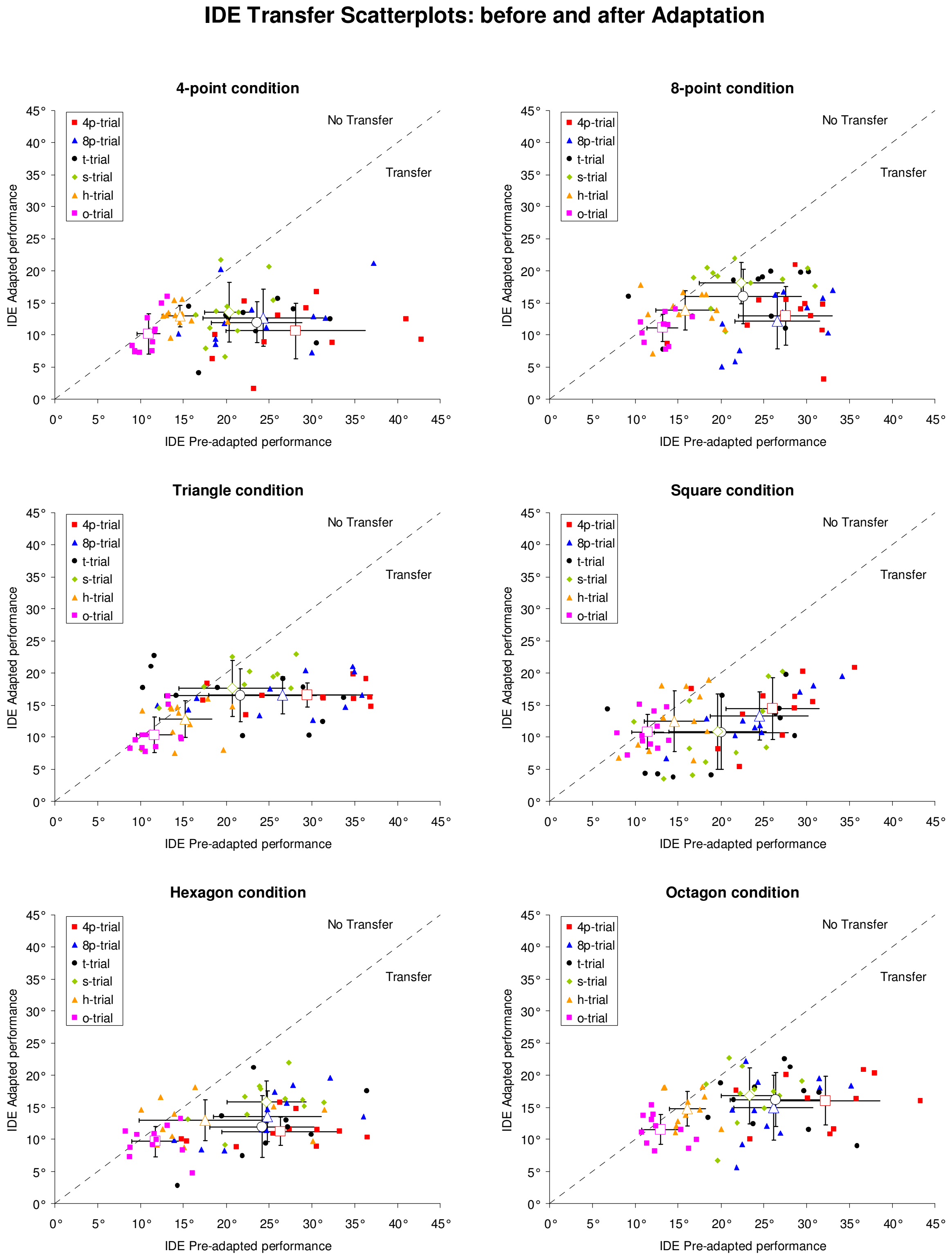

Figure 2.4 shows IDE performance plotted as perforamce before training (x-axis) against performance after training (y-axis) on each condition seperately. Each sub-graph depicts IDE performance of the subjects in that particular condition for all the trial-types (see legends), as well as the group average plus standard deviations.

Overall, analysis revealed a main effect of training $F_{(2,59)} = 492.590$, $p < .001$. Showing that IDEs during naïve, i.e. undistorted baseline and adapted performance (after training) were smaller than IDEs during pre-adapted (i.e. distorted) baseline. In addition, we found a main effect of trial-type ($F_{(5,56)} = 75.997$, $p < .001$), meaning that direction errors were different per trial-type. Participants in the 4- and the 8-point conditions showed adapted performance for both point trial-types as well as the triangle and square trials. In contrast, they only showed minimal adaptation for the hexagon and octagon trial-types. The single subject and group averages (crosses with group SD's) are close to the centerline, representing errors of the same magnitude on both pre-adapted and adapted performance. Participants who trained on the polygon shape trials showed similar behavior on the 4-point, 8-point, triangle and square trial-types, whereas the hexagon and octagon trial-types showed minimal adaptation. Finally, a significant interaction between level of training*trial-type was found ($F_{(10,51)} = 57.088$, $p < .001$), indicating that the differences between trial-types depend on the level of training.

Naïve performance revealed a main effect of trial-type ($F_{(5,56)} = 24.713$, $p < .001$), showing that errors on both discrete trials were smaller under normal conditions than the discontinuous movements. More specifically, both 4-point and 8-point trials had smaller errors than the triangle and square trials ($p<.01$), which had larger errors than the hexagon and octagon trials ($p < .001$). These differences in direction errors under normal (undistorted) conditions suggest that the discrete trials are easier to perform than the discontinuous trials. The magnitude of the errors between the 4-point and 8-point trials were similar as to the errors between triangle and square, and hexagon and octagon. This might suggest that these movements are relatively close together when it comes to difficulties in performance. Performance before training (pre-adapted) also revealed a main effect of trial-type ($F_{(5,56)} = 110.051$, $p < .001$). Here direction errors showed an opposite effect when compared to naïve performance. The hexagon and octagon trials had the smallest errors compared to all other trialtypes ($p < .001$). Triangle and square did not differ from each other but were smaller again than both point trial-types ($p < .001$). These results show that the 'easier' movements (discrete) are disrupted more by the rotation distortion than the slightly more complex movements (discontinuous). Adapted performance (after training) also revealed a main effect of trial-type ($F_{(5,56)} = 12.690$, $p < .001$), an effect of condition ($F_{(5,60)} = 6.117$, $p<.001$) as well as a significant trial-type*condition interaction ($F_{(25,300)} = 2.020$, $p<.01$). Analyzing performance per trial-type per condition showed that errors on the octagon trial were the smallest for each condition ($p < .01$). The other trial-types varied in order but were similar within each condition.

Influence of Movement directions

In addition to the planning and accuracy errors, I was interested in the influence of the movement direction. I wanted to know whether there was a difference in performance when participants had to move, for example, from left to right versus up and down. Thus IDEs for each movement direction were compared per trial-type (also see pg 23). On the two discrete movement trials, 4-point and 8-point trial, we found a slight advantage of the vertical movements when compared to the horizontal movements, they were only significant in the 4-point trial (p< .05). The discontinuous movement trials showed an interesting pattern in that the first movement trajectory had the smallest direction error (nr. 1), p<.001 for triangle and square trials and p<.01 for hexagon and octagon trials.

Direction Errors for Individual Movement Directions

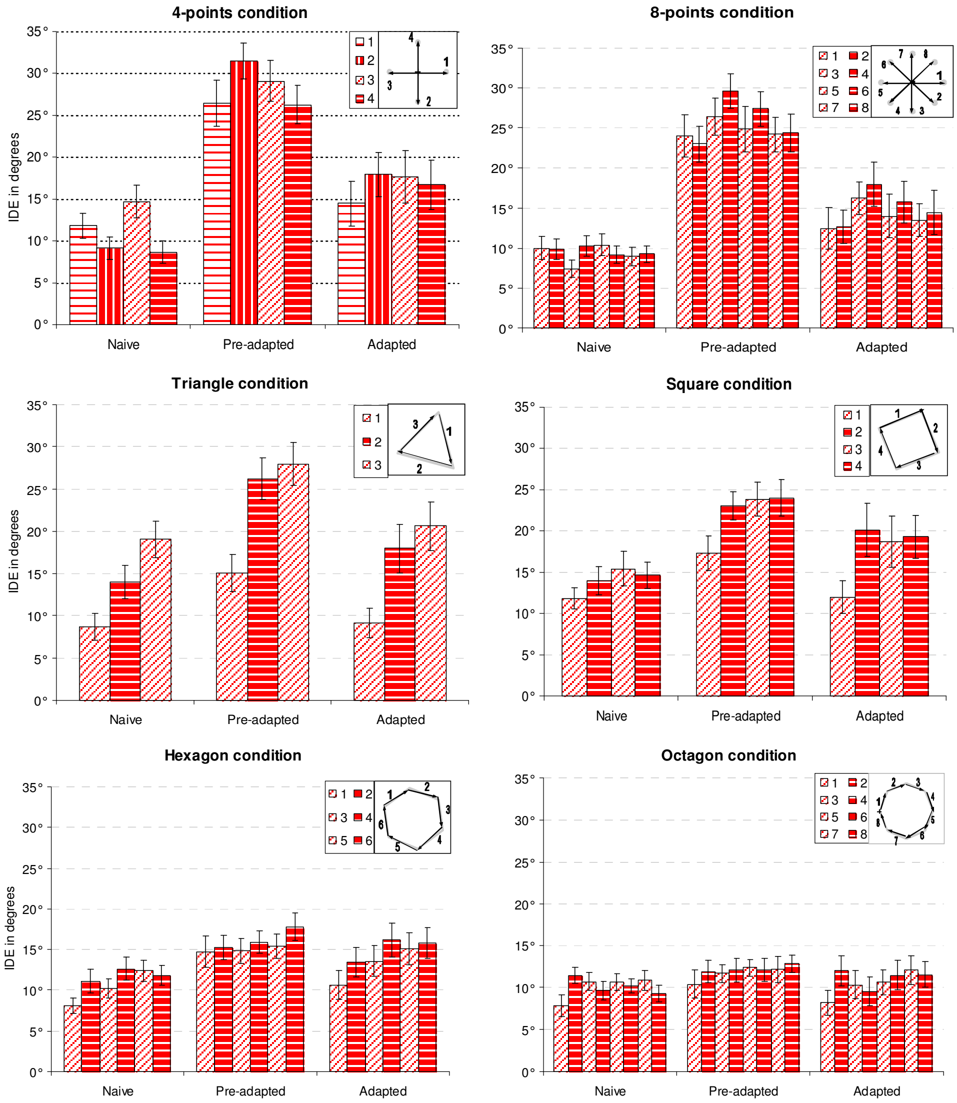

Figure 2.5 represents the IDEs for each condition in each of the movement directions for each level of training. Each movement direction is denoted as a number in the small figure within the graph for each figure and shows the direction error for that specific trajectory from corner to corner, in a clockwise fashion.

2.3.2 Root Mean Square Error

The Root Mean Square error (RMS) represents a measure of accuracy. It shows how well participants follow the 'ideal' line or shape while performing discrete or discontinuous movements. Figure 2.6 shows the time-series adaptation for RMS errors per trial-type, which gives an overall view of performance across training. All trial-types show an increase in RMS error at distortion onset (P) and a gradual decrease thereafter. The errors on the discrete movement trial-types are larger than the errors on any of the discontinuous movement trial-types, of which the hexagon and octagon show the smallest errors.

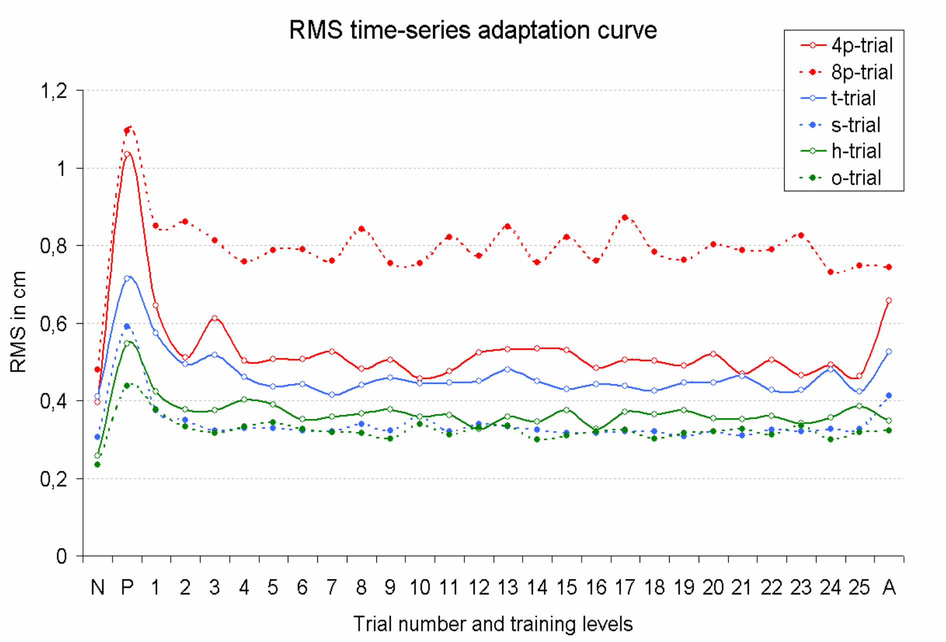

Figure 2.6 shows RMS time-series adaptation curve for all trial-types in relation to the rotation distortion (averaged across participants and conditions), N = Naïve, P = Pre-adaptive baseline, training (matched for number of trials), A = Adapted-test.

Figure 2.7 shows pre-adapted performance plotted against adapted performance for all trial-types per condition, depicting how much participants' performance improved during training. Overall we found a main effect of training: $F_{(2,59)} = 146.226$, $p < .001$, with naïve and adapted RMS being significantly smaller than pre-adapted RMS ($p < .001$). Naïve RMS and Adapted RMS were also significantly different ($p < .001$). Further analysis revealed a main effect of trial-type ($F_{(5,56)} = 105.883$, $p < .001$) as well as a significant training*trial-type interaction ($F_{(10,51)} = 4.179$, $p < .001$). Comparing the different trial-types for naïve baseline, revealed a main effect of trial-type ($F_{(5,56)} = 86.796$, $p < .001$). The accuracy errors (RMS) were largest on the 8-point trial when compared to all other trial-types ($p < .001$). RMS errors on the 4-point and triangle were similar but were smaller than on the hexagon and octagon trial ($p < .001$).

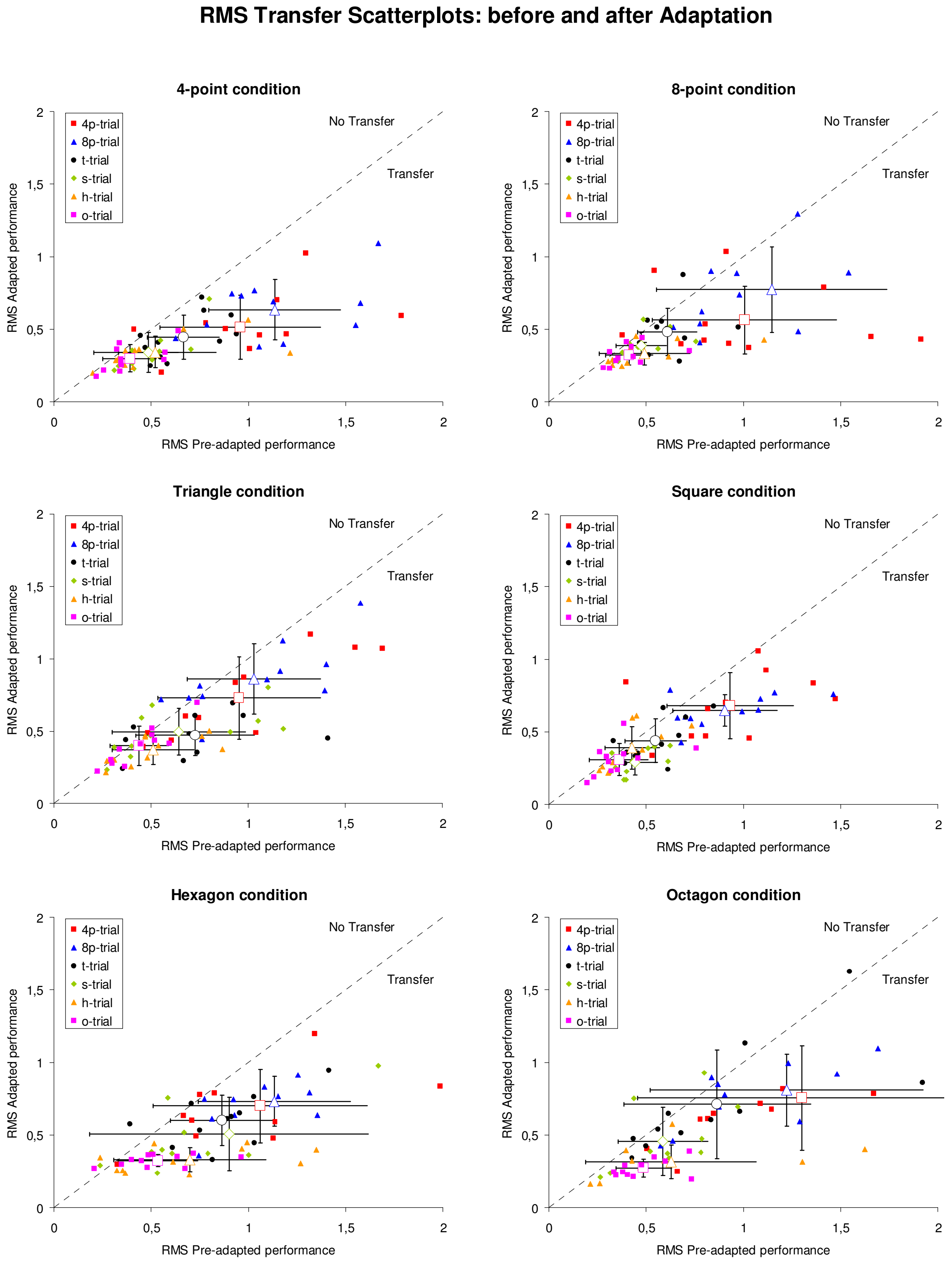

Figure 2.7 shows RMS performance plotted as perforamce before training (x-axis) against performance after training (y-axis) on each condition seperately. Each sub-graph depicts RMS performance of the subjects in that particular condition for all the trial-types (see legends), as well as the group average plus standard deviations.

Results show that when it comes to accuracy the hexagon and octagon are clearly preferred, whereas shapes as the triangle and square as well as discrete movements are performed less accurately. Pre-adapted performance also revealed a main effect of trial-type ($F_{(5,56)} = 66.763$, p< .001). As for the errors on each of the trial-types, performance on the octagon resulted in the smallest errors (p< .01), then hexagon and square trials (p< .01). Next in line were triangle and 4-point trial (p< .001), followed by the largest RMS error on the 8-point trial (p< .001). Results showed that discrete movements are performed less accurate than shapes when participants face a rotation distortion. RMS errors during adapted performance resulted in a main effect of trial-type ($F_{(5,56)}$ = 79..454, p< .001). Overall the accuracy was highest (small errors) for the octagon and hexagon trials, p< .05 for discrete trials and p<.001 for triangle and square trials.

2.3.3 Mean Velocity

A main effect of training was found for mean velocity, $F_{(2,59)}$ = 79.104, p< .001, more specifically subjects moved slowest during pre-adapted training (P) and fastest during adapted training (A). There was no effect of condition, meaning that subjects in one condition performed similar on the same trial-type as subjects in another condition. A clear, yet unsurprising, main effect of trial-type was found ($F_{(5,56)}$ = 62.094, p< .001). Subjects moved significantly faster during pointing-trials than during any of the shape trials, but did not differ significantly within a movement category, i.e. velocities for point-trials and shape-trials were similar (see Figure 2.8). Additionally, subjects get significantly faster with training, the velocities on any of the movement types is fastest after training.

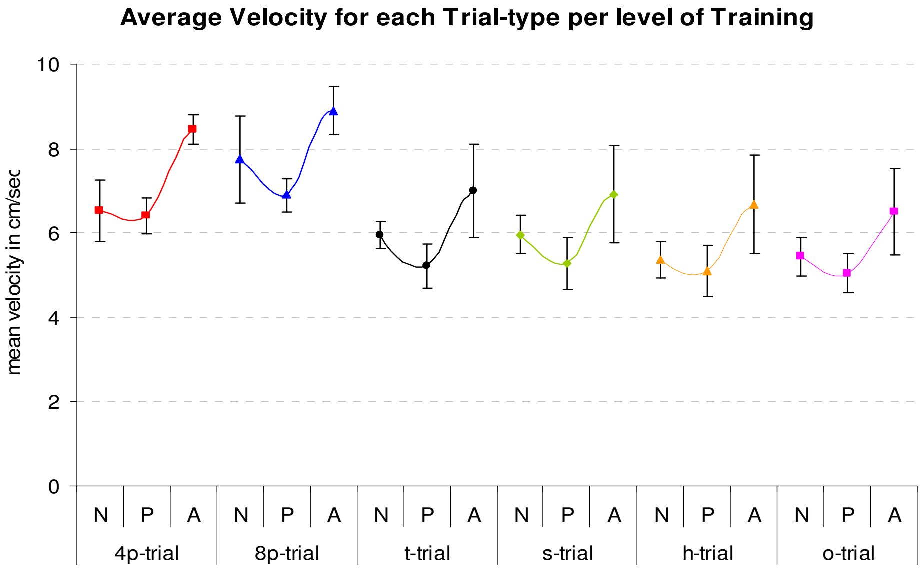

Figure 2.8 shows the Mean Velocities for each trial-type (averaged across conditions) per level of training (N = naïve, P = Pre-adapted and A = Adapted performance).

2.4 Discussion

The aim of the current study was to discover how a rotation distortion was learned and generalized on discrete and discontinuous drawing movements. We manipulated movement kinematics by imposing a 45° rotation distortion on the visual feedback while participants performed movements in the various categories. The definition of the movement categories used here derived from Schmidt and Lee (2005). The current experiment used variants of both discrete and discontinuous movements. The discrete movements were movements with a clear start- and end-position, here the drawing of a straight line between the center cross and a target position. These movements were rather easy and performed relatively quickly. The discontinuous movements consisted of a number of discrete movements strung together, in the current task the drawing of a triangle, square, hexagon or octagon. Discontinuous movements were more complex because each end-point was also a new start point and each corner involved a change of direction.

I proposed the idea that the influence of the rotation distortion was tied to the amount of feed-forward and feedback components used for the planning and control of the movement. The influence of feed-forward and feedback components on movements has been discussed for several years. The forward models stated that a movement is planned before movement onset (Keele & Posner, 1968; Elliott & Allard, 1985; Bhavin & Shimojo, 2002), whereas feedback models proposed a real time comparison between hand and target (Hinton, 1984; Flanagan et al., 1993). The last developed model, the hybrid models, allowed both components to contribute to the movement plan and movement control. Stating that forward components contribute to the formulation of a basic plan before movement onset, which are continuously monitored by feedback. I suggested that there should be a difference in the influence of the distortion on discrete and discontinuous movements. If participants rely more on feedback components than the influence of the distortion should be less disruptive because the motor plan is adapted through a closed-loop system. This would be the case for discontinuous movements, which rely on a basic feed-forward plan and more on feedback components to connect all the lines. The error measurements used in the current study, initial direction error and root mean square error should be able to differentiate between these two components. The initial direction error is the movement direction error at the start of the movement, which is based solely on feed-forward planning, whereas the root mean square error is the averaged deviation from the ideal line or shape including feedback components.

Overall results showed that naïve performance was similar in all conditions with small direction and accuracy errors. Participants only made small direction errors, which were most likely due to the novelty of the task, in performing drawing movements on a horizontal tablet while viewing the pen movements on a vertical screen. Both direction and accuracy errors increased drastically upon first exposure to the 45° rotation distortion. Especially, discrete movements showed large errors in initial direction and deviations from the straight path. The direction errors on both trial-types belonging to the discrete movements (e.g. 4-point and 8-point trial-type) were larger than the direction errors on any of the trial-types from the discontinuous movement category (e.g. triangle, square, hexagon and octagon). More importantly, on the hexagon and octagon trial-type both error measurements showed only a small error increase. Similarly, accuracy performance decreased (RMS errors increased) in all trial-types at first exposure although the effect was relative to the movement type. The largest accuracy errors again occurred for discrete movements, then for the triangle and square and the hexagon and octagon had the smallest RMS errors.

The minimal effect of the distortion on the hexagon and octagon shape was rather unexpected. The movements needed to draw either shape were part of the discontinuous movement class, and the influence of the distortion on the triangle and square shapes was substantial. So what caused this rather minimal effect of the distortion on the hexagon and octagon shape? There are only two big differences between the triangle and square versus the hexagon and octagon, which might contribute to this effect. Firstly, the latter two shapes can be seen as more complex discontinuous shapes because they consisted of more connected discrete movements than the triangle and square. One might argue that complexity increases with the number of discrete movements connected together. Further, the angles of the corner in the triangle and square were 90° or less, whereas the angles of the hexagon and octagon were 90° or more. It might be possible that changes of directions with a 90° angle or smaller are more difficult than changing directions with more obtuse angles. Perhaps the more obtuse the angles the closer the movements needed to draw the shape are to the continuous movement class, which should rely even more on feedback and thus be even less disrupted by the distortion (see Chapter 3).

The study showed that especially discrete movements were heavily influenced by the rotation distortion. The planning errors (IDEs), which did not rely on feedback, were large for discrete movements, largest of all movement categories. This underlined the idea of a full forward movement plan for discrete movements, resembling the ballistic component of a movement (Woodworth, 1899). As Woodworth stated, the ballistic component of a movement does not rely on feedback unless the movement is rather slow. Then a second component, the current-control phase allows visual feedback to make fine corrective adjustments to the movement as needed. Thus the first, ballistic part of the movement relies on open-loop control, only allowing adaptation to the rotation by ‘remembering’ the error and adjusting subsequent movements to the same target (Krakauer et al., 2000), whereas the second part, the current-control phase allows for closed-loop control. This makes sense in light of the current data; participants perform discrete center-out movements quickly and adjust their movements in subsequent trials. In addition, the discontinuous shapes are more interconnected discrete movements, which need both feed-forward and feedback components.

The current study had one minor constraint, namely movements in contrast to other studies occurred in a 2D space and used a stylus to perform movements. Several studies showed effects of constrained movements by use of a tool, such as a joystick, manipulandum or stylus (Desmurget, Jordan, Prablanc & Jeannerod, 1997). The paths created when using a tool were different from the unconstrained 3D counterpart. More specifically, when subjects used a tool, thereby restricting their plane of movement (i.e. fewer degrees of freedom) they can follow a straight and invariant path irrespective of the instruction to move from a start position to a target as quickly and accurately as possible, or to do the same while tracing a straight line. However, when the same task is performed without constraint, movement paths in the ‘free’ condition (not following the straight line) were much straighter. The curvatures of the movements deviated slightly from the perfect straight line during naïve performance, but were negligible.

Influence of Movement direction

The influence of movement directions have been shown to be of influence on movement accuracy. Studies showed that oblique lines are more difficult to draw than horizontal-vertical lines (Broderick & Laszlo, 1987; Laszlo & Broderick, 1985). Such an effect might be due to the horizontal-vertical biases in our surrounding environment. Although studies showed that these biases are strong in children (Bayrakter, 1985; Bryant, 1974; Freeman, 1980; Freeman, Chen & Hambly, 1984; Ibbotson & Bryant, 1976) but becomes less influential with age (Bayrakter, 1985; Ibbotson & Bryant, 1976; Williamson & McKenzie, 1979). The current results revealed a clear preference for horizontal-vertical movement directions over oblique movement directions. This was especially true for discrete movements and somewhat less for the discontinuous movements.

In addition, discontinuous movements showed an interesting pattern. Namely, the direction error made on the first movement part (i.e. from the start position to the first corner), showed the smallest error, whereas for subsequent movements the error gradually increased. This pattern occurred on all training levels, i.e. naïve, pre-adapted and adapted performance. It seemed as if the movement plan was very good for the first movement part, but those for subsequent parts were not as well developed or perhaps not fully developed. What occurs during a movement, which consists of interconnected discrete movements? Do participants plan the movement in segments? Alternatively, is the momentary pause to change direction a problem?

A study by Baraduc & Wolpert (2002), showed that changing the start and arm position to begin a new movement disrupts the previously established movement plan and or already learned adaptation. This might mean that participants while moving experience the brief pause with the change of direction as a 'new' movement, which in turn needs a new movement plan. This the generation of a new movement plan might take longer than they actually have time. Although participants were not instructed in the current experiment to perform movement within a specific time, the movement itself e.g. the tracing of a triangle, does not invite for long pauses. So now the question remains, do participants plan a movement sequentially, that is do they plan the first straight trajectory and then the next planning from corner to corner or rather do they plan the whole movement but are not able to incorporate the distortion past the first trajectory? If assuming that participants plan trajectories in segments, then each corner indicates a new start position, as well as a new arm position from where a new movement plan has to be generated and performed (Baraduc & Wolpert, 2002). Even though the movement is of a discontinuous nature (momentary stops are included) there is only a minimal amount of time to form a new plan, which might lead to a not fully adapted movement plan revealing increases in the error that hardly decreased with training.

Movement Generalization

The final question I asked focused on transfer of learning or generalization across movement categories. Training a particular movement under specific circumstances generally leads to transfer of a skill. I was interested in whether this transfer also occurs between movement categories, which makes sense in the light of the flexibility of the human movement system. If we would not be able to interact with our environment flexibly, we would not be able to transfer skills to new situations. Table 2.1 shows the relative transfer percentages for each movement category (averaged across the different trial-types). Within each movement category, the learning was around 80%, whereas the amount transferred to another movement category varied slightly. Participants training on one of the two discrete trial-types (e.g. 4-point or 8-point trial-type), were able to generalize 58% of their learned knowledge to discontinuous movements (e.g. triangle, square, hexagon or octagon trial-types). Training on one of the discontinuous trial-types allowed a skill transfer of 74% to discrete movements. These percentages show that we are able to transfer a relatively large amount of the skill to another movement, it is only 10-15% less than when we stick to a movement within the same movement category.

This finding is rather important because it shows the high flexibility and adaptability of the human movement system. It allows us to push a 'new' coordinate frame to a higher level, where other movements are able to use it to adapt their movements. It would be interesting to see, how much further such a transfer can be pushed. Whether it holds for pointing to grabbing, grabbing to walking or even transfers into different workspaces?

Table 2.1 Adaptation across Movement Categories in percent

Movement Categories			
		From	
		Discrete	**Discontinuous**
To	**Discrete**	88%	74%
	Discontinuous	58%	81%

In conclusion, the current study provided more insight into movements of different types, i.e. movements that require different execution and/or planning mechanisms. Our main data replicated results from numerous earlier studies using distortions (Stratton, 1897a, 1897b; Kohler, 1955; Ingram et al., 2000; Jakobson & Goodale, 1989; Bock, 1992; Abeele & Bock, 2003; Rosenbaum & Chaiken, 2001; Krakauer et al., 2000; Baraduc & Wolpert, 2002; Prager & Contreras-Vidal, 2003; Wang & Sainburg, 2005) and extended these to discontinuous movements. Moreover, accuracy and direction results confirmed the hypothesis that more complex movements, e.g. discontinuous movements, rely more on feedback components (and closed-loop control) and thus are less disrupted by a rotation distortion than discrete movements which rely mainly on feed-forward components (and open-loop control). The current results also led to new questions, such as the effect of a rotation distortion on the third movement category, the continuous movements.

CHAPTER 3

Adaptation of Discrete and Continuous Movements

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3.1 Introduction

One of the fundamental properties of the human brain is its ability to adapt to changes, be they intrinsic (e.g. growth and aging) or extrinsic (e.g. changing environment). Changing the environment can have profound effects. Imagine lifting a cup in a weightless room or lifting a cup made of lead. Such environmental changes lead to changes in our movement system. Moving a cup made of lead is far different than moving a normal cup. Our sensory systems have to learn how to deal with this transformation. Throughout the years studies showed that human subjects adapt their movements or movement trajectories, following either kinematic (visuomotor) or dynamic transformations, to environmental changes through practice (Conditt et al. 1997; Dizio & Lackner 1995; Flanagan & Rao 1995; Flanagan & Wing 1997; Flash & Gurevich 1997; Goodbody & Wolpert 1998; Held & Freeman 1963; Kitazawa, Kimura & Uka, 1997; Lackner & Dizio 1994, 1998; Lacquaniti & Maioli 1989; Sainburg, Ghez & Kalakanis, 1999; Shadmehr & Mussa-Ivaldi, 1994; Wolpert et al., 1995a, 1995b).

In the previous chapter, we studied a kinematic distortion on two different movement classes, discrete and discontinuous movement class. Results showed that we adapt rather well to a rotation distortion on both movement categories and that there is a fair amount of transfer to the other movement category. The different shapes, however, that we used to represent the discontinuous movement category (triangle, square, hexagon and octagon) showed profound differences in performance. The triangle and square showed similar adaptation patterns as discrete movements, but the hexagon and octagon did not. The distortion only had a minimal effect on these two shapes. Hence, I suggested that the complexity of the latter two movements (due to the shape) is larger and requires more feedback during movement execution. Most likely, the movements will be performed slower than a discrete movement, allowing these feedback loops to provide information to the ongoing movement. This in turn should allow for better online control and thus less disruption of the movement by the distortion.

To investigate this effect more fully, the current experiment tested the last movement category, continuous movements. Continuous movements are movements that have no identifiable beginning or end, the movement continues until it is voluntarily stopped (Schmidt & Lee, 1999; 2005). The circle represents a continuous movement where stopping is not required. In addition, the change of direction is fluid compared to a triangle, for example. This is, of course, part of the movement, but I wanted to account for more abrupt changes of direction. Therefore, I designed two more shapes, a star-shape with 4 and 8 bell-curves. The shapes went through the same target positions but different directions as in the 4-point and 8-point trials. That is they used 4 or 8 anchor points through which a curved line was drawn (see Figure 3.1). Thus, the current experiment compared performance on discrete (4- and 8-point) and continuous (4-curve, 8-curve and circle) movement tasks. Expected was, that participants adapt to the kinematic distortion during training (Fukushi & Asche, 2003). Further, I suggest that continuous movements, due to their complexity, need feedback loops right at the beginning of the movement execution and rely less on the feed-forward component. Verschueren, Swinnen, Cordo & Dounskaia (1999) showed that participants constantly use visual feedback to control the expected drawing with the actual drawing. When participants notice the kinematic distortion, they start to monitor the mismatch between the actual and the expected movement correcting the movements accordingly. Therefore, the direction errors caused by the rotation distortion should be relatively small, especially when compared to the discrete movements. Additionally, smaller errors in accuracy were expected because again, the feedback would allow participants to use online corrections.

3.2 Methods

Subjects

One hundred right-handed students from the Ruhr University Bochum participated in the study. All participants were naïve as to the purpose of our study and had no motor deficits. I divided participants equally among the 5 conditions: 4-points, 8-points, 4-curve, 8-curve and circle trial. The experimenter explained the task and setup before participants signed an informed consent, which the local Ethics Committee approved. Participants received a fee of 10 euro for participation.

Material and Apparatus

See the experimental setup as described in the Methods of Chapter 2.

Task and Procedure

The experiment used five conditions defined by the specific trial-types, categorized in two movement categories: (1) center-out point-trials and (2) continuous shape-trials. The center-out point-trials consisted of either 4 or 8 points distributed at equidistant intervals in a circular fashion (for a detailed description also see Methods of Chapter 2). Participants were asked to move from the center cross to one of 4 or 8 points displayed on the screen. Continuous shape trials consisted of three different shapes with a certain number of ‘smooth’ corners: two star-shaped figures with 4- or 8-curves and a circle (see Figure 3.1). Participants started their movement at the cross and traced the shape clockwise.

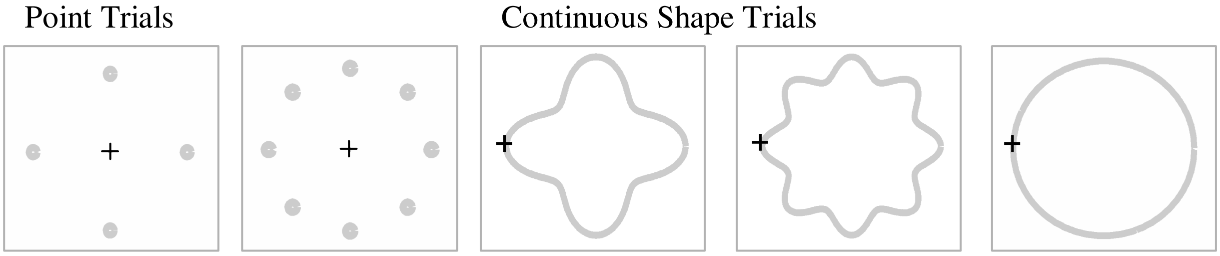

Figure 3.1 Center-out point and Continuous shape trials. From left-to-right: 4-points, 8-points trial, 4-curve trial, 8-curve trial and circle trial.

Data Analysis

For a more detailed description of the Data Analysis, see Methods of Chapter 2.

I measured ***Initial Direction Error*** (IDE), ***Movement Directions***, ***Root Mean Square Error*** (RMS), and ***Mean Velocity*** (VEL). In addition, ***movement directions*** were defined. For the center-out point-trials, I defined movement directions in angles from the center cross in the four cardinal and four diagonal directions. The horizontal movement to the right was defined as 0° e.g. movement direction 1, continuing clockwise with 4 movement directions for the 4-point trial (at 90° intervals) and 8 movement directions for the 8-point trial (at 45° intervals). The movement directions for the continuous trials were defined as the direction of movement on a point 15 pixels away from the start cross (which is the same boundary at which the direction error is measured). Finally, the ***percentage of Adaptation*** was computed using the initial direction errors, allowing us to see how large the adaptation was for learning from naïve to adapted performance, corrected for the error increase after distortion onset. I computed the percentage of adaptation using the equation ***(pre-adapted – adapted)/(pre-adapted – naive)*100***, a 100% adaptation indicates that performance before and after training was similar. Effects were statistically analyzed using repeated measures ANOVA with levels of training and trial-types as within factors. The levels of training were naïve- and pre-adapted baselines, and adapted-test performance. Trial-types were the trial-types used in the current experiment e.g. 4-points, 8-points, 4-curve, 8-curve and circle. Between factors consisted of condition, defined as the matching trial-types used during the adaptation training, as well as the direction of movement (in IDE analysis only). In addition, for easier comparison in the graphs across the different trial-types I averaged the number of trials for all trial-types to a total of 25. Post-hoc analysis used a Bonferonni correction ($\alpha = .05$).

3.3 Results

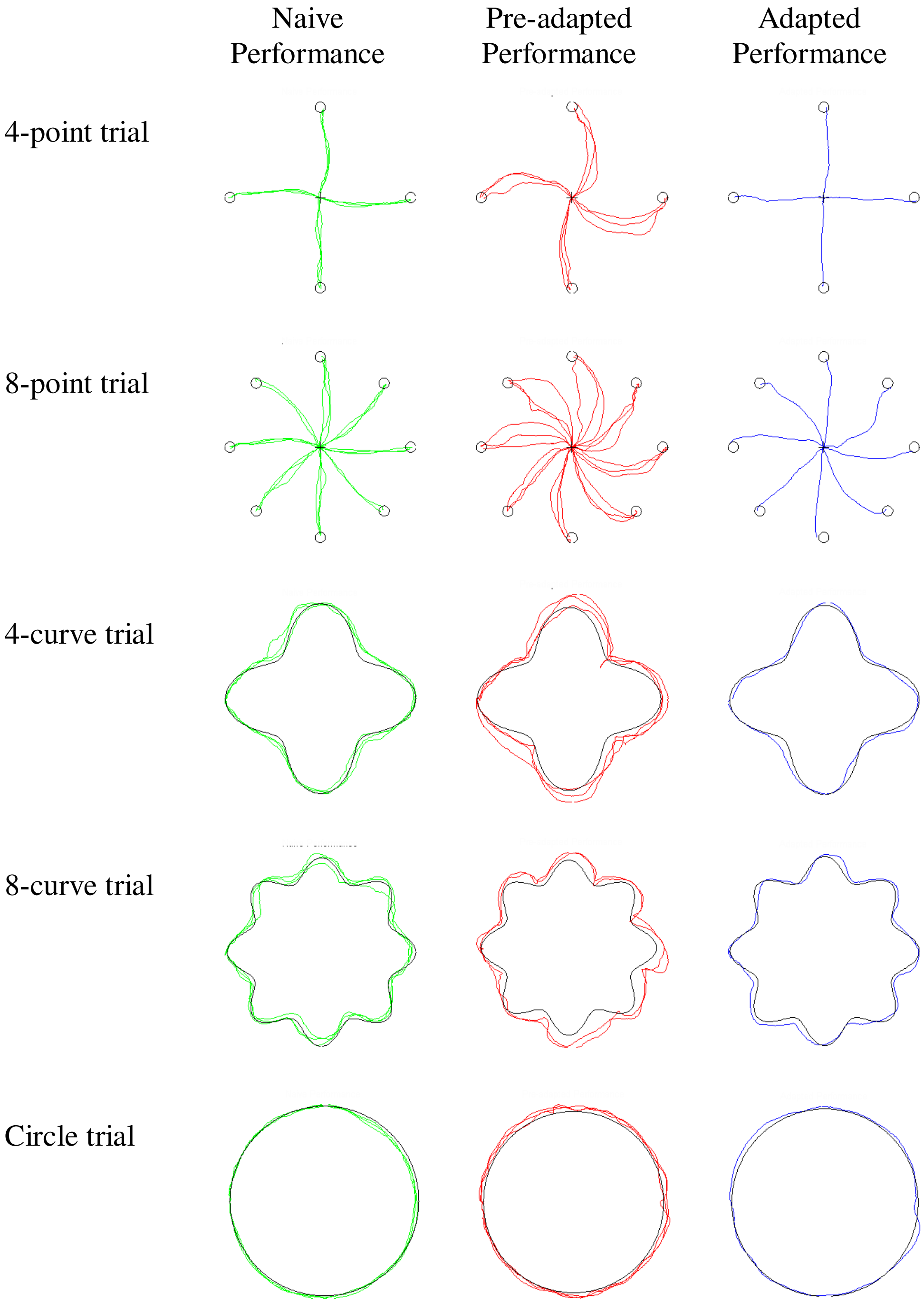

Figure 3.2 shows a full data set of a single subject for all trial-types for each level of training: Naïve performance (green, left column), Pre-adapted performance (red, center column) and Adapted performance (blue, right column). The black shapes represent the different targets.

Figure 3.2 displays an example of the performance of a typical subject throughout the experiment. It shows the subjects' performance on each trial-type during each of the three training levels: Naïve, Pre-adapted and Adapted performance. The data set of the single subject show the typical results, performance is quite good in all naïve trial-types, the green lines are very straight and closely follow the original (black) shapes. When faced with the 45° rotation for the first time (pre-adapted performance) performance changes drastically. The subjects' lines were curvier and diverged further from the original shapes, especially in the two point trial-types. Remember that after pre-adaptation the subject trained one specific trial-type for an extensive time. In the current example, the subject trained the 4-point trial 50 times to adapt to the rotation (200 movements, 50 trials x 4 directions). The last column depicts the adapted performance after training. The lines are straighter than before training, albeit not a straight as in naïve training. Throughout the experiment, we closely observed each subjects performance and again discarded subjects who showed no performance loss when first exposed to the 45° rotation reasoning that these subjects might use a strategy or were less affected by the visual rotation distortion.

3.3.1 Initial Direction Error

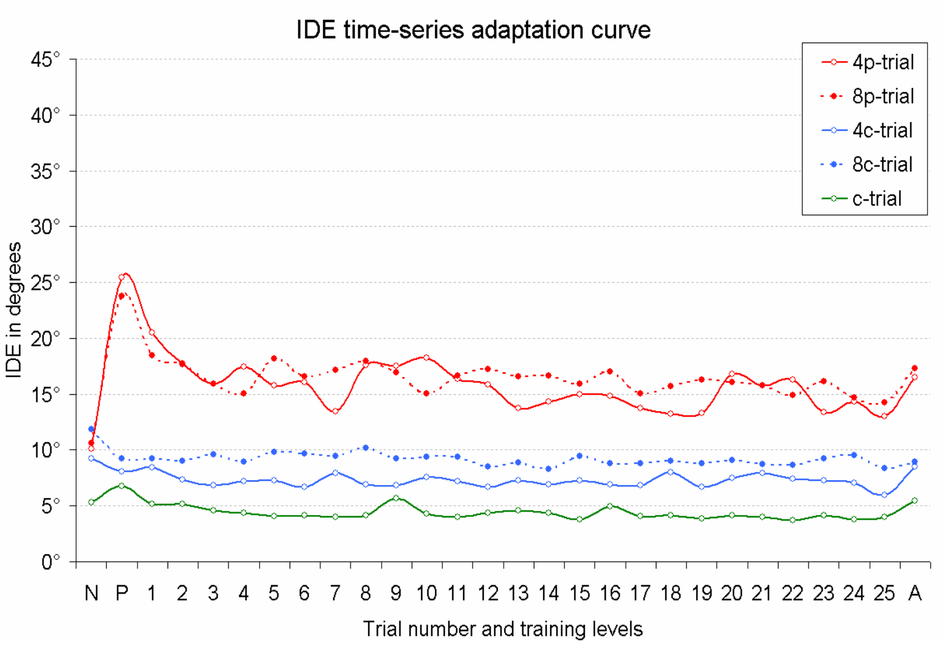

Figure 3.3 shows IDE time-series adaptation curve for all trial-types in relation to the rotation distortion (averaged across participants and conditions), N = naïve, P = Pre-adaptive baseline, training (matched for number of trials), A = Adapted-test.

Figure 3.3 shows a time-series adaptation plot for each trial-type (averaged across conditions and participants) to evaluate overall differences. The first noticeable difference is the absence of a large increase in direction error for the continuous shapes, whereas we do see this increase for the center-out movements. Furthermore, as soon as adaptation-training starts direction errors decrease rather quickly for the center-out trials, participants need around 5 trials to show minimal errors in direction.

Figure 3.4 shows a scatter plot plotting pre-adapted against adapted performance for all trial-types per condition. There is a fair amount of transfer in all conditions for the two point trial-types (4-point and 8-point) but not for the continuous shapes (4-curve, 8-curve shapes and the circle). For the latter the subjects and group averages were close to the centerline or slightly above it, meaning that direction errors made on the different shapes were similar before and after training. However, the data showed that direction errors were small overall, only 5-10° error, which might not be enough to state that participants noticed or were affected by the rotation distortion on these particular shapes.

Statistical analysis revealed a main effect of training, $F_{(2,49)} = 131.383$, $p < .001$, with larger errors on pre-adapted baseline than on naïve baseline and adapted-test. Results showed a main effect of trial-type ($F_{(4,47)} = 210.624$, $p < .001$), as well as several interactions training-level*trial-type ($p < .001$) and a tree-way interaction between training-level*trial-type*condition ($p < .001$). Due to the interactions, we performed separate analyses for each level of training.

Performance during naïve conditions revealed a significant effect for trial-type ($F_{(4,47)} = 52.823$, $p < .001$). Pair wise comparison of the trial-types showed that direction errors during naïve performance were smallest for the circle trial ($p < .001$). IDEs of the 4-curve and 8-curve trials were smaller than on both discrete trial-types ($p < .001$) and performance on the 4-curve was better than on the 8-curve trial ($p < .01$). Comparing trial-types before training (pre-adapted performance) revealed a main effect of trial-type ($F_{(4,47)} = 198.795$, $p < .001$), with large direction errors for both discrete trials (4-point and 8-point trials) but only small errors for the continuous shape trials. Suggesting indeed that continuous shapes rely on the visual feedback and thus the actual error was minimized. As for performance after training, again a main effect of trial-type was found ($F_{(4,47)} = 92.687$, $p<.001$). The errors, even though reduced in comparison to the pre-adapted performance are still largest on the 4-point and 8-point trials.

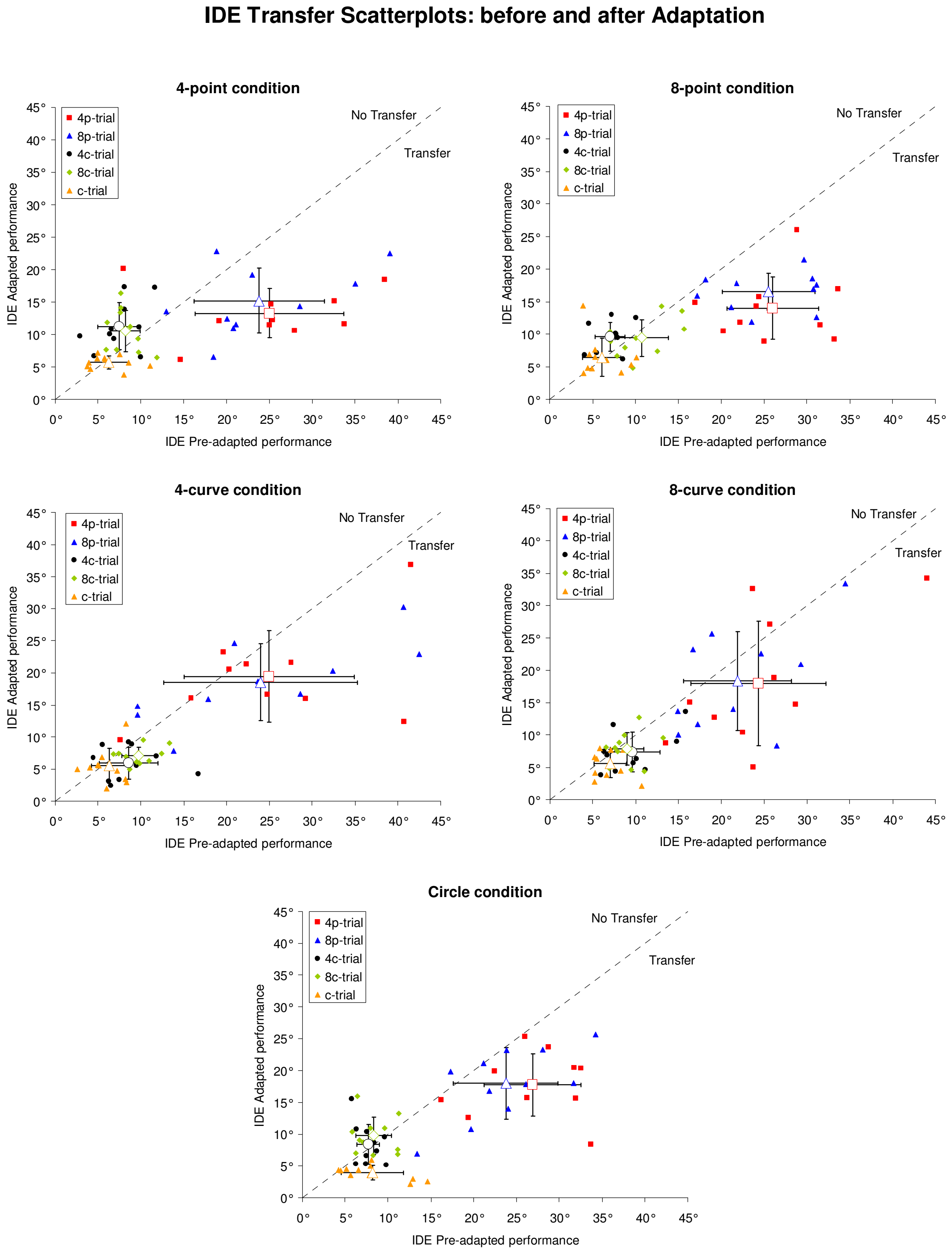

Figure 3.4 shows IDE performance plotted as perforamce before training (x-axis) against performance after training (y-axis) on each condition seperately. Each sub-graph depicts IDE performance of the subjects in that particular condition for all the trial-types (see legends), as well as the group average plus standard deviations.

Influence of Movement directions

In addition to the planning and accuracy errors, I was interested in the influence of the movement direction. Meaning, I wanted to know whether there was a difference in performance when participants had to move, for example, from left to right versus up and down. Figure 3.5 shows the IDEs for each movement direction per trial-type. There is no preference in any of the trial-types for a specific movement direction.

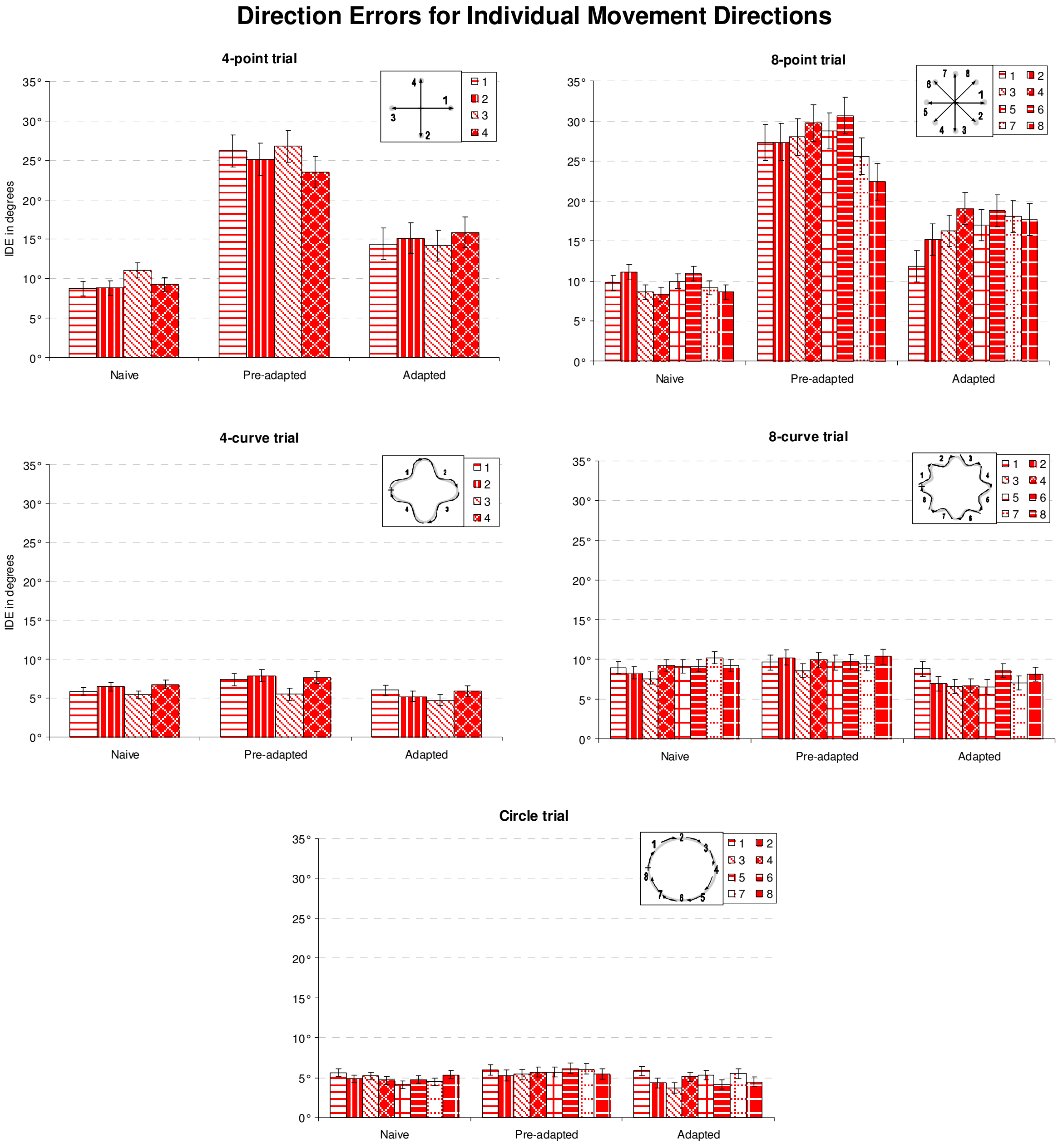

Figure 3.5 represents the IDEs for each condition in each of the movement directions for each level of training. Each movement direction is denoted as a number in the small figure within the graph for each figure and shows the direction error for that specific trajectory from corner to corner, in a clockwise fashion.

3.3.2 Root Mean Square Error

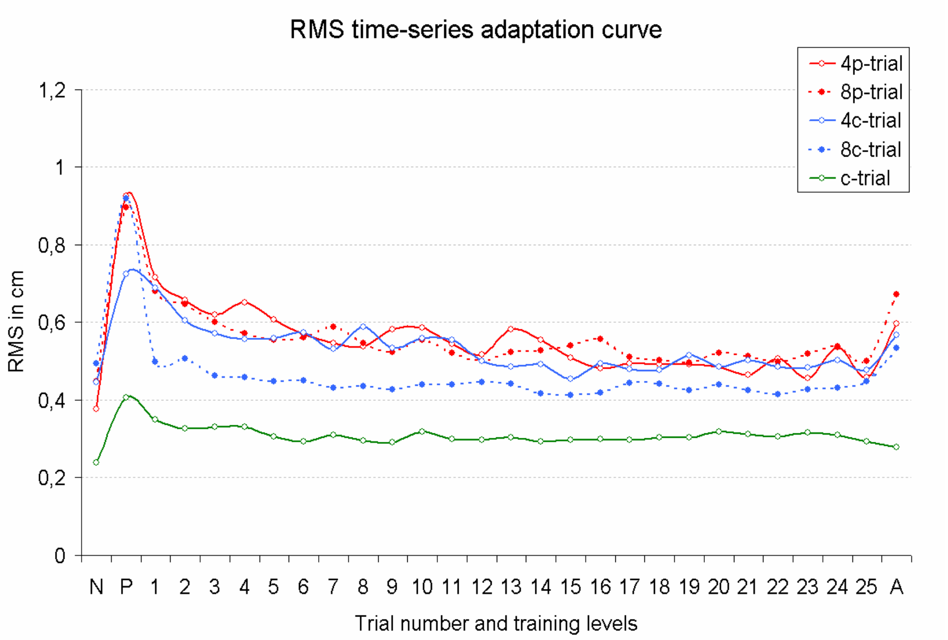

Figure 3.6 shows RMS time-series adaptation curve for all trial-types in relation to the rotation distortion (averaged across participants and conditions), N = Naïve, P = Pre-adaptive baseline, training (matched for number of trials), A = Adapted-test.

The time-series plot (Figure 3.6) shows the performance over time on the different trial-types. Notice the large errors during pre-adapted performance for the discrete and continuous trial-types with the change of direction, but the lack of such an increase for the circle.

Accuracy performance revealed a main effect of training ($F_{(2,94)} = 195.931$, $p < .001$), with small accuracy errors during naïve baseline, a large increase at initial exposure of the distortion (pre-adapted baseline) and a gradual decrease throughout the training period, with small errors during adapted performance. Figure 3.7 depicts the performance between pre-adapted and adapted performance plotted against each other, showing how much participants improved performance during training. In addition, results revealed main effects for trial-type ($F_{(4,92)} = 80.887$, $p < .001$) and for condition ($F_{(4,95)} = 4.973$, $p < .01$). Finally, we found several interactions, training-level*trial-type ($p<.001$) and a tree-way interaction between training-level*trial-type*condition ($p < .01$). Due to the interactions, we performed separate analyses for each level of training.

Naïve performance revealed a main effect of trial-type ($F_{(4,92)} = 50.724$, $p < .001$) Comparison of the trial-types revealed larger errors on the two discrete trial-types than on the continuous trial-types. More specifically, performance on the circle trial resulted in the smallest errors when compared to all other trial-types ($p < .001$). Accuracy of the 4-point trial was better than performance on the 8-point, 4-curve and 8-curve trials ($p < .01$).

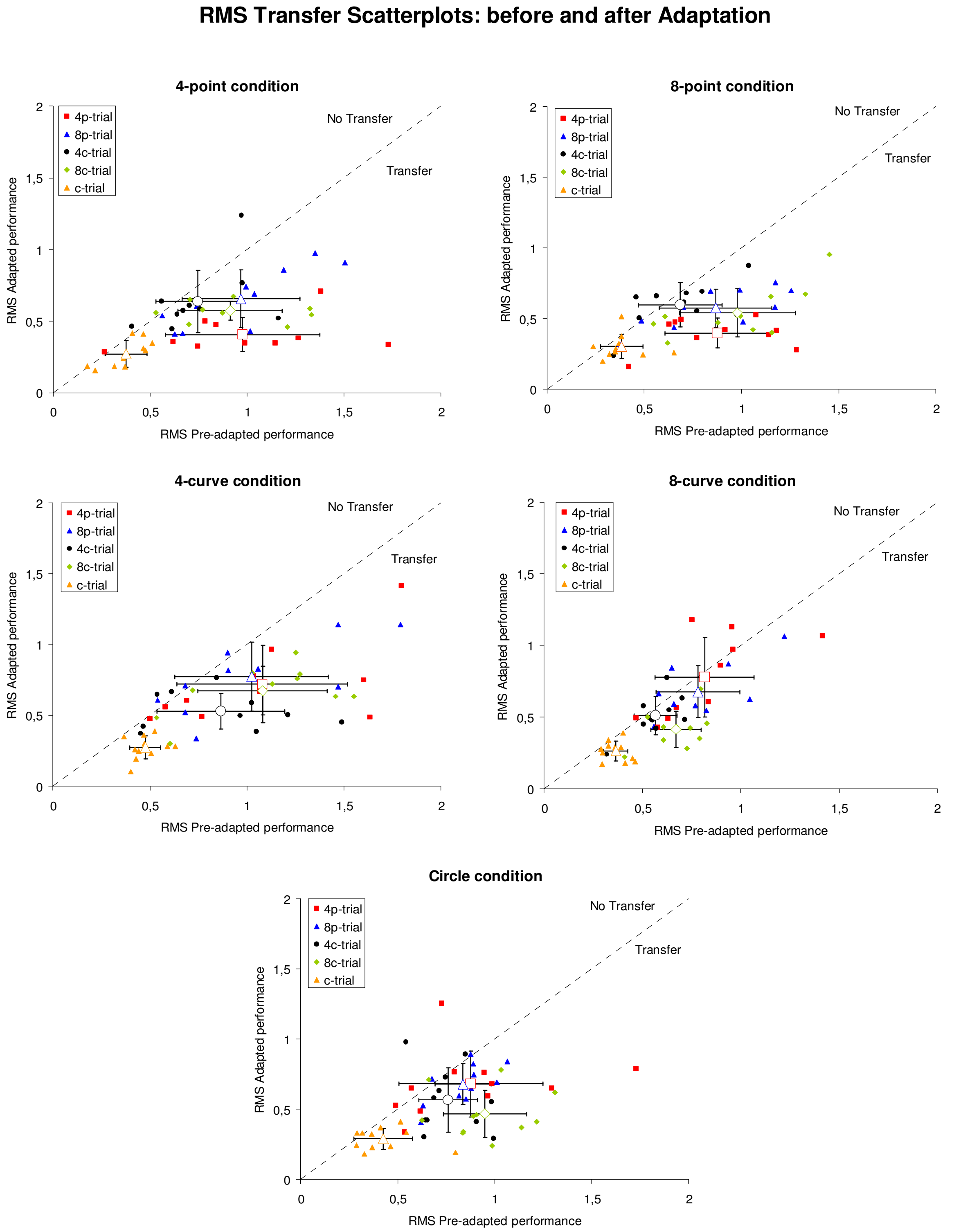

Figure 3.7 shows RMS performance plotted as perforamce before training (x-axis) against performance after training (y-axis) on each condition seperately. Each sub-graph depicts RMS performance of the subjects in that particular condition for all the trial-types (see legends), as well as the group average plus standard deviations.

Finally, performance on the 8-point trials was better than performance on the 8-curve trials (p< .05). Results showed that drawing a circle was relatively easy when compared to the other two continuous movements and the discrete movement trials. Performance before training (pre-adapted) revealed a main effect of trial-type ($F_{(4,92)} = 25.243$, $p < .001$), with the smallest deviation errors for the circle trial than both discrete trial-types ($p < .001$) as well as both curve-trials, $p < .001$ and $p < .05$, for 8-curve and 4-curve trial respectively.

Performance after training (adapted) also showed a main effect of trial-type ($F_{(4,92)} = 85.490$, $p < .001$). Accuracy on the circle trials was better than on any of the other trial-types ($p < .001$). Further, performance on the 4-curve and 8-curve trials was better than performance on both discrete trials ($p < .001$). Overall results show that the rotation distortion disrupts performance on discrete movements as it did in experiment 1. Similarly, continuous movements with changes of direction, as in the 4-curve and 8-curve trial, also show that the rotation distortion disrupts performance on these trials, whereas a continuous movement such as a circle is hardly affected (see Figure 3.7).

3.3.3 Mean Velocity

Analyzing the mean velocities revealed a that mean velocities during adapted performance were higher than during naïve or pre-adapted performance, revealing an effect of training (see Figure 3.8). Moreover, the effect of trial-type was significant ($F_{(4,92)} = 66.828$, $p < .001$), showing that velocities on the center-out trials were similar in performance, and both were higher than mean velocities on the shape trials. An effect of condition was not found, but several interactions were significant; training*condition interaction ($p < .01$) and trial-type*condition ($p < .001$).

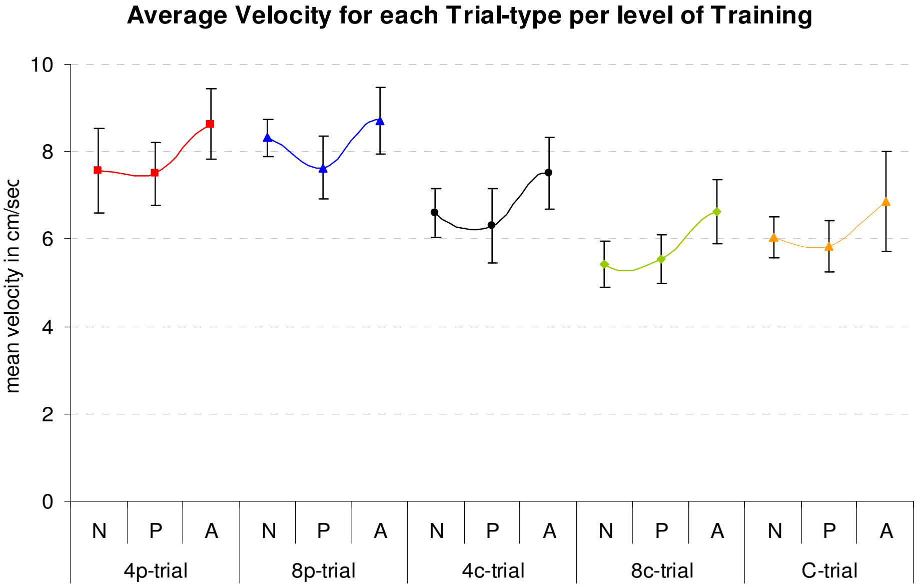

Figure 3.8 shows the Mean Velocities for each trial-type (averaged across conditions) per level of training (N = naïve, P = Pre-adapted and A = Adapted performance).

3.4 Discussion

The focus of this study was to discover what the effect of a rotation distortion was on discrete and continuous drawing movements. The previous chapter looked at learning and generalization on discrete and discontinuous movements revealing that discontinuous movements are slightly less influenced by a 45° rotation of the visual feedback, leading to the idea that continuous movements (as defined by Schmidt & Lee, 1999; 2005) should be even less influenced. Results replicated findings for discrete movements (see previous chapter) in adaptation research (Conditt et al. 1997; Dizio & Lackner 1995; Flanagan & Rao 1995; Flanagan & Wing 1997; Flash & Gurevich 1997; Goodbody & Wolpert 1998; Held & Freeman 1963; Kitazawa et al. 1997; Lackner & Dizio 1994, 1998; Lacquaniti & Maioli 1989; Sainburg et al. 1999; Shadmehr & Mussa-Ivaldi 1994; Wolpert et al. 1995a, 1995b). However, performance on the continuous movement tasks revealed only small direction errors for continuous movements but a ‘normal’ performance decrease in accuracy.

The main finding was that direction errors increased with the onset of the distortion for both discrete trials, but not for the continuous movement trials. In contrast, accuracy (RMS) did decrease at the onset of the distortion for all trials but least for the circle. Both error measures gradually decreased throughout training to an asymptotic level similar to naïve performance. Zelaznik & Lantero (1996) tested participants in a repetitive blind circle-drawing task. Showing that participants did not need a visual reference to keep form in the blind-circle drawing task. This fits with results from the current study, in that participants were able to keep form, while not being able to observe their arm movement and receiving rotated visual feedback. The findings lead to the idea that participants make use of a sort of ***internal model*** or ***movement plan*** for the circle and thus would not need the actual visual reference.

The use of an internal model for planning and executing movements is widely accepted (Wolpert et al., 2001). Evidence favors the cerebellum as the most likely place of such an internal model, even if the specifics of the model are still under debate. One group of researchers argues in favor of an ***internal forward model*** (Miall et al., 1993; Jordan, Flash & Arnon, 1994; Wolpert et al., 1995a; 1995b), whereas the opposing group argues in favor of an ***internal inverse model*** (Saltzman, 1979; Atkeson, 1989; Uno, Kawato, Suzuki, 1989; Hollerbach, 1990). The forward model makes rapid (causal) predictions of the sensory consequences of motor commands (review in Wolpert & Ghahramani, 2001; Wolpert et al., 2001), delaying the predicted sensory feedback so it can be compared directly with the actual sensory feedback[7] (Miall, et al., 1993). The inverse model on the other hand translates information about the desired trajectory into the required motor commands (review in Wolpert & Ghahramani, 2001; Wolpert et al., 2001; Kawato & Gomi, 1992). Patients with peripheral sensory neuropathy (e.g. proprioceptive deafferentation) produced uncoordinated arm movements when performing movements with their eyes closed, in contrast to when performing movements with normal vision which markedly improved performance (Sainburg et al., 1993). The authors proposed that the loss of proprioception disrupted inter-joint coordination. Evidence regarding this idea comes from a study testing the effects of muscle and tendon vibrations on circle drawing (Verschueren et al., 1999). Their findings showed that the CNS used proprioceptive information related to elbow and shoulder rotation to control movement of the hand, accomplishing the spatial characteristics of the task. Thus, even though the internal model in the cerebellum may predict movement paths, it is not completely accurate and relies on sensory feedback.

In line with this, the current findings showed that movement paths were highly influenced by the visual feedback of the hand position (RMS errors), for both discrete and continuous movements (Note, that visual feedback only occurred by means of the screen, participants had no direct visual feedback of their hand and arm). Our planning data (IDE errors) showed a feed-forward component of such an internal model, direction errors decreased very rapidly after exposure to the distortion, showing that participants already incorporate the distortion into their movement calculations. In our data, it is hard to discern whether these findings are due to an internal model or due to a developing strategy. Then again, a strategy might allow the internal model to update its parameters using a feed-forward command and in turn using sensory feedback for movement control i.e. correct movements online and update the movement model for subsequent movements (Krakauer et al., 2000).

Movement Generalization

Further, I addressed the question of transfer of learning. Transfer of learning refers to the effect of experience in a prior task on the performance of learning a novel task (Schmidt & Lee, 1999; 2005). In the current case, whether learning of a rotation distortion on a, for example, 4-point center-out task improved or interfered with performance on the circle tracing task. To investigate this more thoroughly, I computed a percentage of adaptation; ***(pre-adapted – adapted)/(pre-adapted – naive)*100***, a 100% indicates complete adaptation.

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[7] Sensory feedback is provided by afferent neurons, carrying information from the hand and arm towards the central nervous system, leading to a perception.

Showing performance from naïve to adapted performance, corrected for the error increase after distortion onset.

Table 3.1 shows that within category adaptation was rather good, 76% for the discrete movements and 93% for the continuous movements. Note that the continuous movements were not disrupted by the onset of the distortion, thus participants had no real need to adapt, the percentage most likely shows some learning through practice. It is however interesting to see that practicing discrete movements did facilitate performance on the continuous shapes. Participants trained on discrete movements are just as good as participants who trained on continuous movements. This shows that participants transferred the knowledge learned in the discrete task and used it for continuous drawing movements. The opposite transfer was less efficient, only 41% of the knowledge learned while performing continuous movements could be used to accurately perform discrete movements.

Table 3.1 Adaptation across Movement Categories in percent

Movement Categories			
		From	
		Discrete	**Continuous**
To	**Discrete**	76%	41%
	Continuous	93%	93%

3.5 Movement Generalization - concluding discussion

In the last two chapters, I continually discussed transfer and generalization across movement skills. Table 3.2 shows a combined table of percentages for both experiments, allowing a better comparison. Note, that I averaged the percentages from both experiments on the discrete trials. In addition, I split the discontinuous trial-types, since the triangle and square differed significantly from the hexagon and octagon. The data within each category show a good adaptation percentage. The data across categories are more diverse. Kinematic knowledge trained on discrete movements transfer very well to continuous movements, well to discontinuous movements, specifically the triangle and square and less well to the hexagon and octagon. Continuous movements however, only show a small transfer to discrete movements. The discontinuous movements (triangle and square) show a moderate generalization to discrete movements and to the hexagon and octagon. Practice on the latter two trial-types, also leads to a moderate to good transfer to discrete movements as well as to the triangle and square trials. It seems very hard to transfer knowledge from continuous movements to discrete. Perhaps because the two movements are both at the continuum end as proposed by Schmidt & Lee (1999; 2005). It would be interesting to see how the adaptation transfer would be from discontinuous to continuous and vice versa. One would expect it to be also moderate.

Table 3.2 Adaptation across Movement Categories in percent

			Movement Categories			
				From		
			Discrete	**Discontinuous**		**Continuous**
			4-point, 8-point	Triangle, Square	Hexagon, Octagon	4-curve,8-curve,circle
To	**Discrete**	4-point, 8-point	**82 %**	68 %	79 %	41%
	Discontinuous	Triangle, Square	71 %	**99 %**	83 %	?
		Hexagon, Octagon	44 %	51 %	**90 %**	?
	Continuous	4-curve,8-curve,circle	93 %	?	?	**93%**

CHAPTER 4

Transfer of learning with and without Visual Targets: the role of position information

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4.1 Introduction

The pioneering work by Woodworth (1899) showed that vision plays an important role in goal-directed movements. To date a large body of data has been accumulated which focuses their main questions on the influence of vision on goal-directed movements. Participants faced many different situations; moving, pointing or aiming without visual movement feedback (Meyer et al, 1988), in the dark (Elliott, Carson, Goodman & Chua, 1991) or blindfolded (Chieffi & Gentilucci, 1993; Wing et al., 1986). The study by Elliott and colleagues (1991) also studied the influence of the presence of the target but without movement feedback (movement in the dark) and showed that the target position eliminated accuracy errors as compared to a no target condition. Related studies investigated the influence of observing the limb during movement and found vision of the hand to be critical in a reaching task (Carlton, 1981a; 1981b) whereas other did not find changes in movement kinematics when vision of the limb was occluded (Jakobson & Goodale, 1991).

The current experiment also aimed at discovering the influence of target information, with vision of the moving limb being occluded but receiving visual feedback through the screen. Participants performed on a simple line drawing task (discrete center-out movement) in either 4 or 8 direction or by drawing a circle (continuous movement). The target was shown briefly on the screen and extinguished shortly before movement onset. Throughout the experiment, vision of the hand was occluded, but visual feedback of their movement was provided on the screen (as when drawing with a regular pen). Participants were not able to see their starting position, but could infer it through internal loops, as well as the movement itself. They only received secondary information about their movement trajectory upon the screen, but could not compare their movements to an actual target position or shape. As in other experiments, participants performed this task under normal undistorted conditions and while receiving 45° distorted visual feedback.

We postulated that being able to briefly view the target position or shape prior to movement allowed for basic planning of a movement plan on which they could rely. Thus expecting that participants would rely more on internal feedback loops and that their movements would not be as ‘disrupted’ by the rotation as when a visual reference was actually present. They could use their visual movement feedback to some extent to control the movements, but the so-called ‘error detection mechanism’ detecting deviations between the actual and planned hand path should be ignored since no reference path was given.

Motor planning and motor control rely heavily on visual and proprioceptive feedback. Continuous visual feedback gives information about the target, initial arm position, ongoing movement and position of the arm after movement. The need for visual information on movement control is evident, being able to see the target allows for adequate planning and continuous updating of the movement component. In the current study, participants faced a simple task of moving a stylus across a graphical tablet (as in writing) in a center-out fashion and while tracing a circle. After measuring a baseline without distortion (naïve), a 45° clockwise rotation distortion disrupted movement planning. In addition, we eliminated visual information of the target, half of the participants, the ***visual-target group***, received the visuomotor task where the respective targets were constantly visible. The other half, the ***no-visual-target group***, received the task were visual targets were removed at movement initiation. In addition, participants only received indirect feedback about their hand position, i.e. they could not see their arm directly but could see a cursor representing their hand position. These visual restrictions should eliminate or disrupt position information or updating of position information since participants are no longer able to compare their hand position to the target position. We wanted to know whether having a visual landmark or not changed the adaptation process, whether learning takes longer when no visual target was present or whether participants learned by means of subsequent trials.

4.2 Methods

Subjects

Seventy-eight right-handed students of the Ruhr University Bochum participated in the study on two groups: a ***visual-target*** and a ***no-visual-target*** group. Each group consisted of three conditions: 4-points, 8-points, and circle, each condition held the same number of participants. All participants were naïve as to the purpose of our study and had no motor deficits. The experimenter explained the task and setup before participants signed an informed consent, approved by the local Ethics Committee. Participants received a fee of 10 euro for participation.

Material and Apparatus

I used the same experimental setup as described in the Methods of Chapter 2.

Task and Procedure

The procedure followed the same basic protocol as described in the Methods of Chapter 2. I used three conditions defined by the specific trial-types, of which two center-out point-trials (4-point and 8-point-trial) and a tracing trial (circle trial). The center-out point-trials consisted of either 4 or 8 points distributed at equidistant intervals in a circular fashion. The circle trial consisted of a continuous circle laid over these points (Figure 4.1). Naïve and pre-adapted baseline performance was acquired followed by an adaptation phase in one of the three conditions followed by a final test for all trial-types. We compared performance across two groups, a ***visual-target group***, and a ***no-visual-target group***. Half of the participants received stimulus presentation with a constant view of the target (e.g. Visual-target group), whereas targets in the no-visual-target group disappeared at movement onset. A visible cursor allowed participants to see their position on the screen while vision of the arm was hidden from view during all trials.

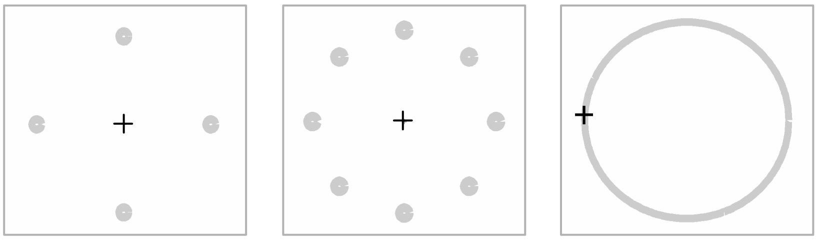


Figure 4.1 shows the computer screen as it appears during the task, with 4-point-trial, 8-point-trial and the circle-trial.

Data Analysis

For each trial, I measured the ***Initial Direction Error*** (IDE) from the starting cross as described in Methods of Chapter 2. For data analysis, IDEs were averaged across the different directions in all trial-types. For the circle, the same 8 positions were used as in the 8-point trial. Furthermore, I compressed the number of adaptation trials to 25 trials for all conditions, by averaging over every 2 or every 4 trials in the 8-point and circle condition respectively. Finally, we split the 8-point trial-types into two categories, 8-point-cardinal, for those directions that matched with the 4-point directions and 8-point-diagonal for the four remaining directions. To compare performance between visual-target and no-visual-target groups we performed a one-way ANOVA per training level (naïve and pre-adaptive baselines, training and test) and separately per condition (4-point, 8-point, and circle condition).

4.3 Results

4.3.1 Initial Direction Error

Comparing the two visual target conditions (visual-target and no-visual target group) showed a main effect of group, with smaller direction errors in the no-visual-target group ($F_{(1,96)}$ = 15.914, p<.001). Furthermore, analysis revealed a main effect of training, with naïve and adapted-test direction errors being significantly smaller than pre-adaptive errors ($F_{(2,95)}$ = 393.081, p<.001). Comparison between the conditions resulted in an effect of condition ($F_{(3,96)}$ = 60.140, p<.001). Finally there were two significant interaction effects, one for training*condition (p<.001) and one for training*target-group (p<.01), thus I analyzed the effects per level of condition.

4-point Condition

The top left of Figure 4.2-A, shows performance of the 4-point condition for visual-target (blue) and no-visual-target (red) group. The first three trials display the naïve baseline, where subjects performed center-out movements in four directions without a rotation distortion. I found no main effect for visual-target, meaning there were no significant differences between the two visual-target groups. The next three trials show the pre-adapted trials, where subjects were first exposed to the rotation distortion, the direction error shows a large increase at first and a steady decrease throughout the consecutive trials (adaptation phase) until it reached baseline level again. Again, no significant differences were found between the visual-target groups in performance for pre-adapted, adapted and test in the 4-point condition, indicating that both visual-target groups perform similar across the different training levels. Furthermore, I compared the three training levels; naïve, pre-adapted and test performance for each visual-target group. The training effect revealed significant effects, naïve baseline was significantly different from pre-adapted baseline (p< .001) and pre-adapted from test (p< .001), but naïve and test performance in the 4-point condition were not significantly different for each visual-target group.

8-point Condition; cardinal and diagonal directions

As for the 8-point condition, I split the 8-point condition in two further sub-conditions; 8-point condition for cardinal and 8-point condition for diagonal directions. The cardinal directions matched the directions of the 4-point condition whereas the diagonal directions are completely new. The 8-point condition for cardinal directions, revealed no significant visual-target effects during naïve or pre-adaptive baseline trials. In addition, performance throughout adaptation and test was also not significantly different between the visual-target groups (Figure 4.2-B). As for the 8-point condition for diagonal directions (Figure 4.2-C), no significant differences were found between visual-target groups in initial direction errors during naïve and pre-adapted baselines, or during adaptation and test. Further, I found a main effect of training for both 8-point conditions, with the pre-adaptive baseline being significantly different from both naïve and test performance ($p < .005$), whereas the two latter ones were not significantly different.

Circle Condition

During the circle condition, Figure 4.2-D shows IDEs of participants in both visual-target groups, and displays a striking difference. Participants in the no-visual-target group showed smaller direction errors during naïve and pre-adaptive baselines. Only a slight, not significant, increase at first exposure of the rotation is evident in the no-visual-target group, whereas the visual-target group displays a larger increase in direction error. Even more striking is the sudden drop in the no-visual-target at the beginning of the adaptation phase, which remains constant thereafter. In contrast, the visual-target group performs similar as in the other conditions, with a large increase at first exposure of the distortion and a continuous decrease until test. The IDEs of the no-visual-target group are significantly smaller than those of the visual-target group ($F_{(1,24)} = 82.641$, $p<.001$). In the circle-condition, the main effect of training is only evident for the visual-target group, displaying the significant increase at first exposure and the similar performance in naïve and test. The no-visual-target group displays no effect of learning, since their performance is already at the ‘floor’.

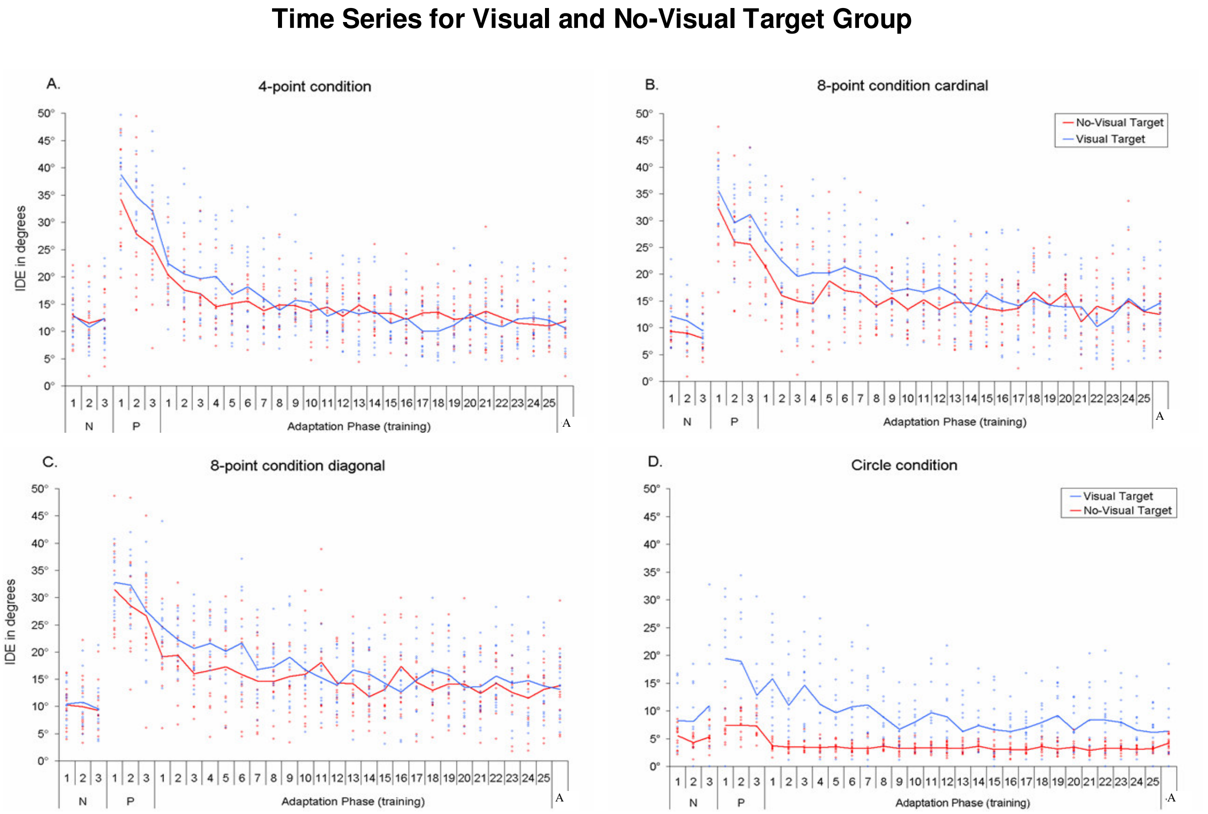


Figure 4.2 shows IDEs for visual-target (blue) and no-visual-target group (red), open dots represent single subjects in the two conditions. Subjects in the (A) 4-point condition, (B) 8-point condition cardinal directions, (C) 8-point condition diagonal directions and (D) circle condition.

4.3.2 *Mean Velocity*

Figure 4.3 shows the results for mean velocity found in the current experiment. The mean velocities were relatively constant for all conditions across baselines, training-phase and test-trials. All conditions showed a slight increase in velocity during the adaptation phase.

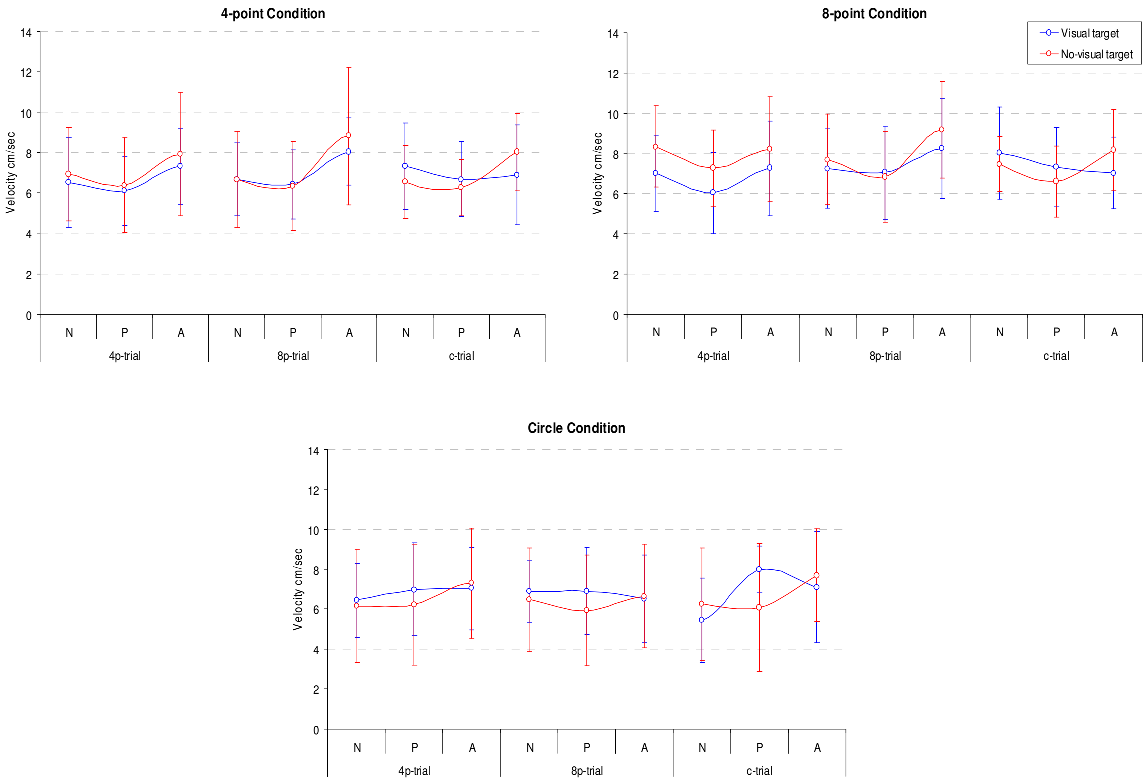


Figure 4.3 shows mean velocity (lines) for both visual-target groups (visual-target = blue, no-visual-target = red) per condition for baselines and test for each of the trial-types.

4.4 Discussion

In the next experiment, I focused more on the internal representation of the movement plan. I asked whether task demands such as, having a visual target to aim at or not, influences performance and or planning during a rotated visuomotor task. The first two experiments showed that if a movement plan was already fully developed before movement onset, the distortion on the visual feedback led to increased errors in performance. The results showed that the more complex a movement (e.g. continuous movements) the more we rely on the visual feedback presented. In theories of visual guidance, commonly describe the mechanism of visual feedback as an ‘error detection mechanism’. The motor system notices a deviation from the actual movement and the expected or planned movement towards the target. It then tries to minimize this error and continuously check the deviation error. Hence, I was interested in what would occur if the reference i.e. the target location or shape was removed. To test this, I compared performance on a visual-target and a no-visual-target group. I only used discrete and continuous movements, but instead of showing the target continuously, the target was removed after a brief period (before movement onset) for half of the participants. Now participants could only rely on the internal plan and partially on their movement feedback (afferent and proprioceptive), but since the latter cannot be connected to a specific target, the 'error detection mechanism' should be relatively abundant. Therefore, I expected fewer errors when no visual target was present. The results showed that the unavailability of the target only mattered in case of the continuous movement. Results showed that having a visual target only made a difference when tracing the circle. Tracing performance of the no-visual-target group on the circle-trial showed a negligible effect of the distortion on the direction errors at distortion onset, and no adaptation effect.

The importance and influence of visual feedback remains disputable in reaching and movement studies. In the study presented here, both groups (visual and no-visual-target group) performed the task without vision of the limb. I measured direction errors shortly after movement onset as a measure of planning. Performance on the center-out movements prior to adaptation, i.e. naïve (undistorted) and pre-adaptive (distorted) baseline were similar in both groups. Direction errors were small during naïve baseline but increased considerably after the distortion onset. This increase was followed by a slow decrease in errors throughout training, eventually reaching an asymptotic level at the end of the adaptation phase. The effect for the circle trial was far different. The onset of the distortion had no effect on the no-visual-target group; direction errors increased insignificantly and returned to the undistorted baseline almost immediately (see Figure 4.2). However, the current results did not match with findings in the previous chapter (chapter 3) where participants performed a visuomotor test using center-out movements and several continuous trials. Participants in that task did not show this increase in direction errors, even though the feedback was continuously on during the experiment. This discrepancy between these two similar continuous tasks might be due to simple subject variations or due to instruction differences. Another reason, might be that in the current study the focus was different. Participants only had to perform movements on 3 different trial-types whereas in the previous experiment they performed movements on 5 different trial-types.

We propose that the current results are due to the visual-target or no-visual-target conditions, meaning different mechanisms were used when there was no landmark or target available. In this case, it was no longer possible to acquire the needed positional information between the hand and target position (Paillard, 1996) because the target was no longer available. Hence, a different strategy had to be employed. Additionally, participants did not receive direct (visual) feedback from the hand, since it was occluded from sight. Participants in the visual-target group compared their screen-position with the visual target, as shown by longer movement times and lower mean velocities (see Figure 4.3), resulting in slightly larger but non-significant direction errors at the beginning of the adaptation phase. Other than that, participants in our study showed no overt problems with the hand being hidden from view. Two concurrent studies (Prablanc et al., 1986; Pélisson et al., 1986) showed that participants were able to complete accurate arm movements without vision of the limb. Nonetheless, arm movements were 3 times more accurate when the target was present throughout the entire movement than when the target disappeared shortly after movement onset. Bédard & Proteau (2003) showed that a cursor representing the hand position on the screen could lessen this information loss, leading to an improved accuracy of the movements. This supports our finding that hiding the hand from vision did not overtly impair participants. The current results demonstrated not only that arm movements could be made without vision of the limb but participants also adapted to a visuomotor distortion while visual feedback of the hand was unavailable.

Removing visual feedback of the hand resulted in slower movements, i.e. lower velocities (Prablanc et al., 1979; Jeannerod, 1984; Prablanc & Pélisson 1990; Jakobson & Goodale, 1991; Berthier et al., 1996) than generally reported in studies where vision of the hand was not prohibited. An additional reason for the slower movements might be that movements in the current experiment were not 3D-pointing movements but rather 2D-drawing movements while holding a stylus. Desmurget and colleagues (1997) showed that constrained movements by use of a tool, such as a mouse or manipulandum, created different paths than unconstrained 3D arm movements. Participants, using a tool, instructed to draw a straight line from a start position to a target drew straighter lines than participants instructed to trace a straight line between the same points. In the current study, participants were instructed not to trace the shape presented on the screen but to draw the shape that was shown. However, in half of the subjects the shapes remained visual during the trial.

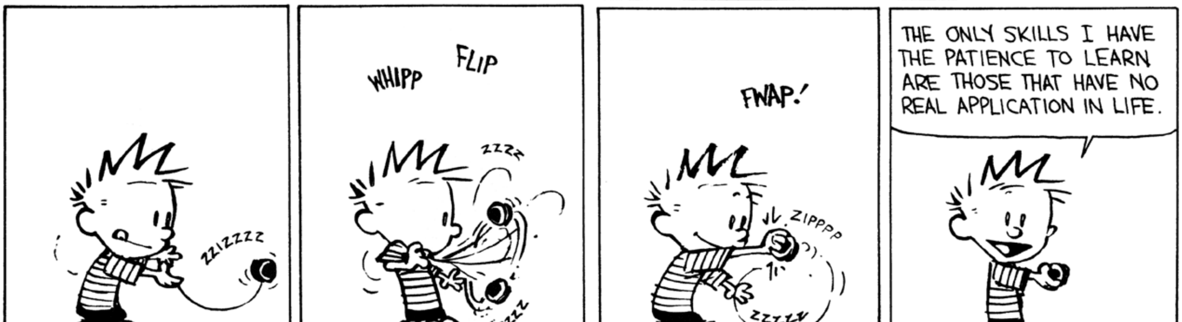
The disappearing of a visual target at movement onset did not reveal any group differences on the discrete center-out movements. Participants' center-out movements were similar in direction errors, velocity and movement time. In contrast, drawing the circle showed marked differences between the two visual-target conditions (visual vs. no-visual target). Participants in the no-visual target condition made smaller direction errors, had higher mean velocities and took less time to complete the movement than participants in the visual-target condition. In addition, the no-visual target group showed no adaptation effect while drawing the circle; the distortion had a small, almost negligible effect on their movements. Seemingly, participants in the no-visual target group simply drew a circle, as instructed, and did not need the visual reference. In fact, being able to see the circle seemed more of a hindrance than a help on the distorted trials. In line with these findings, Zelaznik & Lantero (1996) showed that participants in a repetitive blind circle-drawing task did not need a visual reference to keep form in the blind circle-drawing task. Apparently, a circle is such a well-known figure, that we might have an existing internal program or model for it, consequently not needing the actual visual reference of the circle (Note: circles in both conditions were similar in size and resembled actual circles).

Finally, we suggest that not being able to compare the hand-position directly to the screen-position reduced the influence of online control, participants had to rely more on their ‘internal’ guidance and proprioceptive information because the visual information was not available. In contrast, Elliott & Lee (1995) found that in a pointing experiment using the Müller-Lyer illusion the influence of the target information did not diminish when direct online visual feedback was no longer available. In fact, when he removed visual feedback and visual representation before the movement, the effect was actually magnified. Both studies underline the idea that there are some planning processes before movement onset. In our case, a movement plan was constructed prior to movement, and participants ‘stuck’ to it because there was only limited visual information.

The current results support both the ***hybrid model*** and the ***dual motor model***. Both models allow feed-forward and backward commands to control the movement. The feed-forward command is used to estimate the movement displacements between the location of the hand and the target. This displacement or sensory consequence is then converted into the respective motor command, i.e. inverse modeling. This latter state is the crude movement plan, which unfolds under rigid control i.e. uninfluenced by feedback mechanisms (matching the initial direction errors). Sensory feedback loops become active thereafter. Early loops such a motion information, pick up on differences between the ongoing movement and the direction of the gaze (towards the target). Error signals update the internal movement model, through for example online movement corrections (Pélisson et al., 1986; Prablanc & Martin, 1992; Hoff & Arbib, 1993; Miall et al., 1993; Desmurget et al., 1999). Later loops compare the current location of the hand to the target position. In case of a discrepancy an error signal is issued, generating a series of corrective sub-movements, guiding the hand towards the target (Jeannerod, 1988; Paillard, 1996; Desmurget & Grafton, 2000). Between the estimated movement plan and the sensory feedback loops, we are quite capable of performing movements with great accuracy even if distortions are present. Participants in the current study showed rather quick online corrections when the distortion was active, opposing findings by Krakauer and colleagues (2000) were subjects did not attempt to correct imposed directional errors online but rather used the visual feedback to change the direction of subsequent movements. However, in the current experiment visual feedback was limited, first subjects did not receive visual feedback from the hand and second only half of the participants were able to use stimuli as a visual target. Apparently, not being able to refer to a visual target removed the necessity to correct movements through feedback loops and just kept the internal model of the circle active, which in this case was quite accurate.

CHAPTER 5

Intermanual Transfer on a Visuomotor Task



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5.1 Introduction

Skill transfer or transfer of learning is an important skill to human beings. It allows us to learn a certain skill in a particular situation but when a similar situation occurs we can still perform the skill and do not have to re-learn it. Take the baseball game, players often use a so-called pitching machine to practice their batting skill. The pitching machine is a substitute for the 'real' pitcher. Practicing with the pitching machine does improve the batting performance of players when faced with a 'real' pitcher. This flexibility is extremely important since we rarely face exactly the same situation twice.

Throughout the years researchers asked question as to how much 'knowledge' is transferred and to which extent. Studies revealed two main factors influening the amount transferred. First the amount is rather small and positive unless the tasks are practically identical, and secondly, it depends on the similarity between the two tasks (Schmidt & Young, 1987). The amount of transfer is negligable when the two tasks are completely different (Lindeburg, 1949; Blankenship, 1952). Throughout the years, studies showed transfer effects across workspace (Krakauer et al., 2000; Shadmehr & Mussa-Ivaldi, 1994; Thoroughman & Shadmehr, 2000), to different motor systems (Keele, Jennings, Jones, Caulton, & Cohen, 1995; Grafton, Hazeltine & Ivry, 1998; Kelso & Zanone, 2002), or to the other hand i.e. intermanual transfer (Imamizu & Shimojo, 1995; Thut et al., 1996; 1997; Sathian & Zangaladze, 1998; Temprado & Swinnen, 2005).

In the current experiment, I was interested in the intermanual transfer of an adaptation task. The previous studies already showed that learning was good within each movement category and that there was a good amount of transfer to other movement categories. So now, I wondered whether there would be a positive transfer effect across hands. Participants performed the same drawing task with three different movement categories as before, under normal and under distorted visual feedback. Only one-half of the participants adapted to the distortion with their right hand, whereas the other half adapted to the distortion with their left hand. I expected to find a positive transfer from the dominant (right) hand to non-dominant (left) hand.

5.2 Methods

Subjects

Sixty right-handed students of the Ruhr University Bochum participated in the study across six conditions: 4-points, 8-points, 4-curve, 8-curve, square and hexagon trial, each condition held an equal number of subjects. All participants were naïve as to the purpose of our study and had no motor deficits. The experimenter explained the task and setup before participants signed an informed consent (approved by the local Ethics Committee). Participants received a fee of 10 euro for participation.

Material and Apparatus

I used the same experimental setup as described in the Methods of Chapter 2.

Task and Procedure

The experiment consisted of six conditions defined by the specific trial-types, categorized in three movement categories: (1) center-out point-trials, requiring discrete center-out movements, (2) polygon trials, requiring discontinuous movements, and (3) continuous trials, requiring continuous movements. The center-out point-trials consisted of either 4- or 8-points distributed at equidistant intervals in a circular fashion. The corners of the shape trials matched the number of directions in the points-trials. The polygon shape trials consisted of a square and an octagon trial, and the continuous trials consisted of two star-shaped figures with 4- or 8-curves (see Figure 5.1).

The procedure followed the same basic protocol as described in the Methods of Chapter 2. Participants started their movement at the cross and either made a center-out movement towards the target-points or traced the shape clockwise. Participant received both baselines (naïve and pre-adapted) three times, once performed with the right hand and once with the left, resulting in a total of 6 baseline trials for each training level. Subsequently, participants received training with only one hand in one trial-type (e.g. condition), followed by adapted-test performed with both hands. Half of the participants started the procedure with their right-hand, meaning they used only their right hand for adaptation training (Right-hand training group), whereas the other half started the procedure with the left hand, thus receiving adaptation training with their left hand (Left-hand training group).

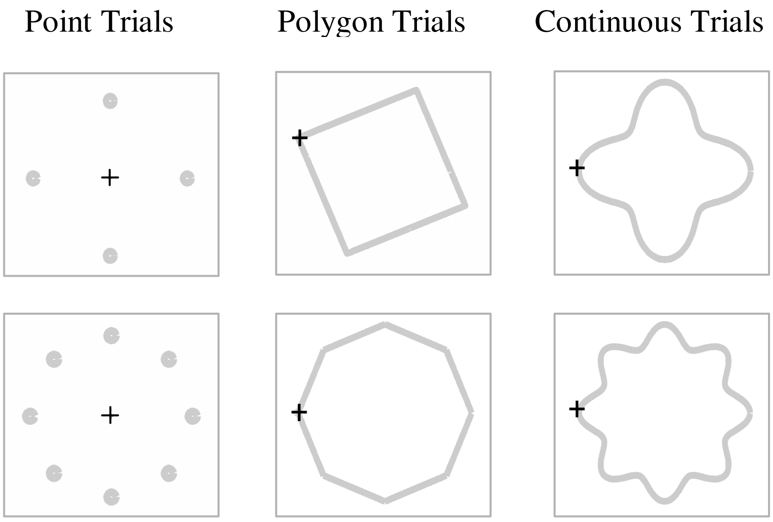


Figure 5.1 shows the two center-out, polygon shape and continuous shape trials.

Data Analysis

We measured ***Initial Direction Error*** (IDE), ***Root Mean Square Error*** (RMS) and ***Mean Velocity*** (VEL). For statistical analysis, we used repeated measures ANOVA with training-level (naïve, pre-adapted, adapted) and trial-types (4-point, 8-point, square, octagon, 4-curve, 8-curve) as within factors, and group (Right-trained vs. Left-trained), hand-used (right- or left-handed trial) and condition as between factors. Post hoc analysis was performed using a Bonferonni correction ($\alpha = .05$). As a measure of generalization we computed a percentage of adaptation using the equation ***(pre-adapted – adapted)/(pre-adapted – naive)*100***. A 100% adaptation indicates that before and after adaptation, performance was similar again. For a detailed description, see Methods of Chapter 2.

5.3 Results

5.3.1 Initial Direction Error

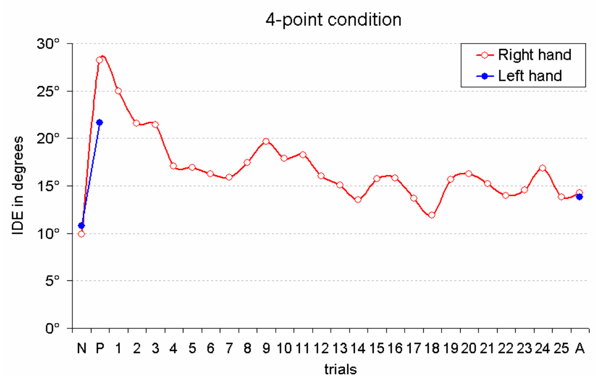
Comparing the two groups, right-hand trained and left-hand trained, across training levels showed a main effect of training ($F_{(2,95)} = 327.919$, $p<.001$) with naïve performance and adapted performance being better than pre-adapted performance (see Figure 5.2), at least for the center-out trials. Moreover, an effect of trial-type ($F_{(5,92)} = 153.482$, $p<.001$) provides a more detailed picture, the center-out movements had an overall higher error than the continuous trials. Furthermore, the effect of condition was significant ($F_{(5,96)} = 3.098$, $p< .05$), showing that performance differed between the different conditions. The analysis revealed no significant effects for group and hand but did reveal several significant interactions. However, I was more interested in the intermanual effects and since the comparison between the right-and left-trained groups did not attain significance, I performed separate analyses for each of the groups.

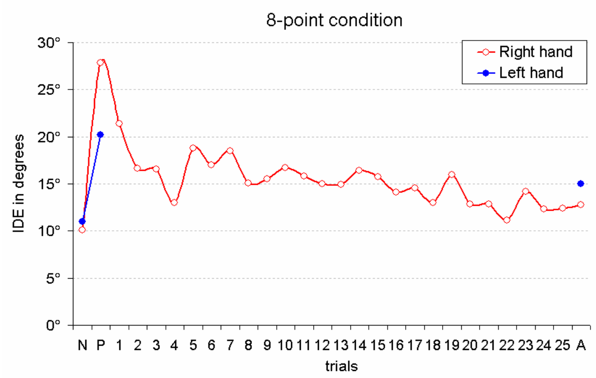
Figure 5.2 shows the performance of both hands for the right and left-trained group (right and left column respectively) per condition (rows). The right-trained group revealed a main effect of training ($F_{(2,47)}$ = 188.334, p< .001), generally with the expected increase for pre-adapted (P) performance. Additionally, the effect of trial-type was significant ($F_{(5,44)}$ = F = 49.737, p< .001). However, the interaction for training*trial-type was significant as well (p< .001), meaning that this training effect is not the same across trial-types. In the current case the error, increase did not appear for both curve-trials and the octagon trial. The effect for condition and hand did not reach significance, meaning that each condition performed similar across the different trial-types and levels of training. More interesting was the results that performance of the left and right hand was not different.

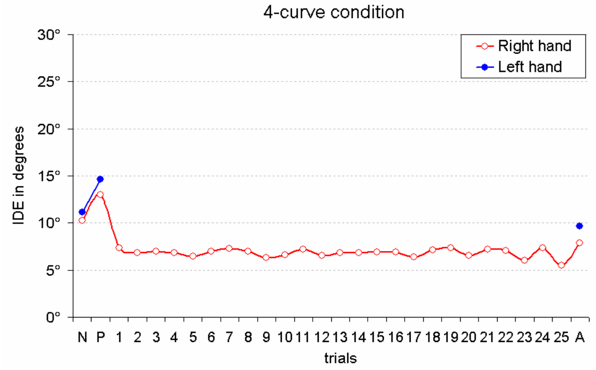
As for the left-trained group a main effect of training was found ($F_{(2,47)}$ = 140.623, p< .001) as well as for trial-type ($F_{(5,44)}$ = 133.025, p< .001). Again, the interaction between training*trial-type was significant (p< .001) showing that when drawing continuous shapes or an octagon with the left hand, there was no increase in IDE at the distortion onset. The remaining trial-types, both center-out trials and the square showed the expected increase at distortion onset, with the gradual decrease in direction errors throughout training. Finally, the effects for condition and hand were not significant for the left-trained group.

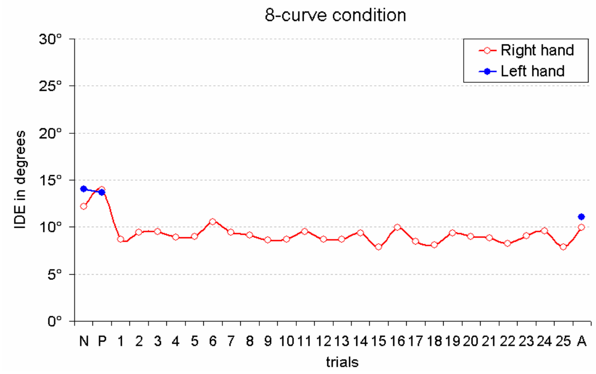
Right and Left hand IDE Performance per Trial-type

Trained with Right hand

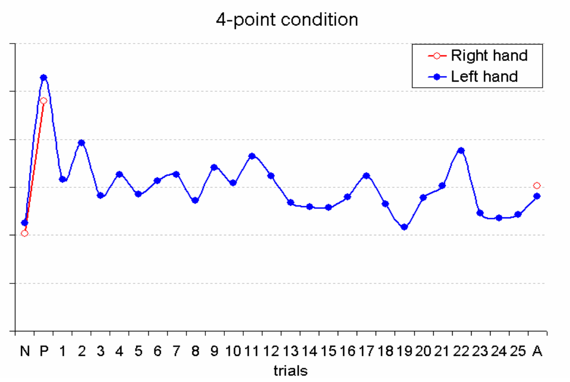


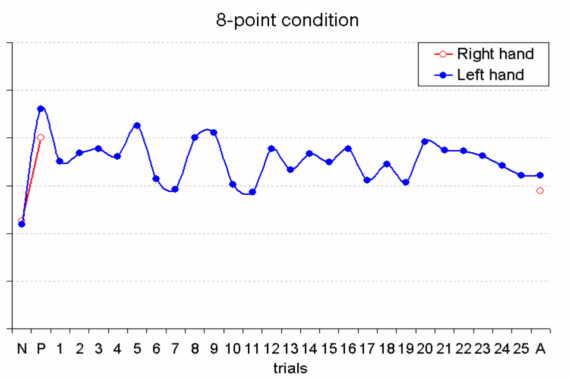


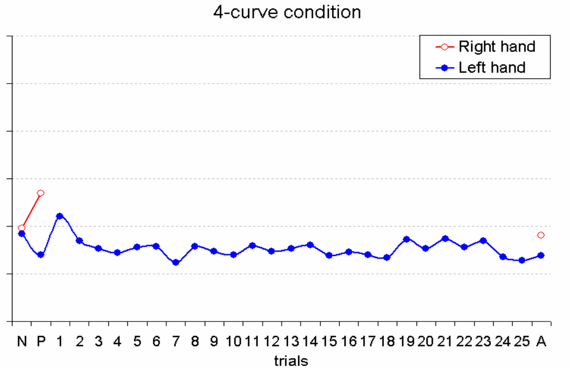


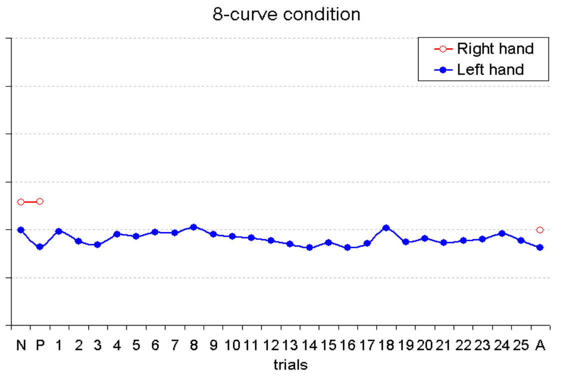


Trained with Left hand









Right and Left hand IDE Performance per Trial-type (Continued)

Trained with Right hand **Trained with Left hand**

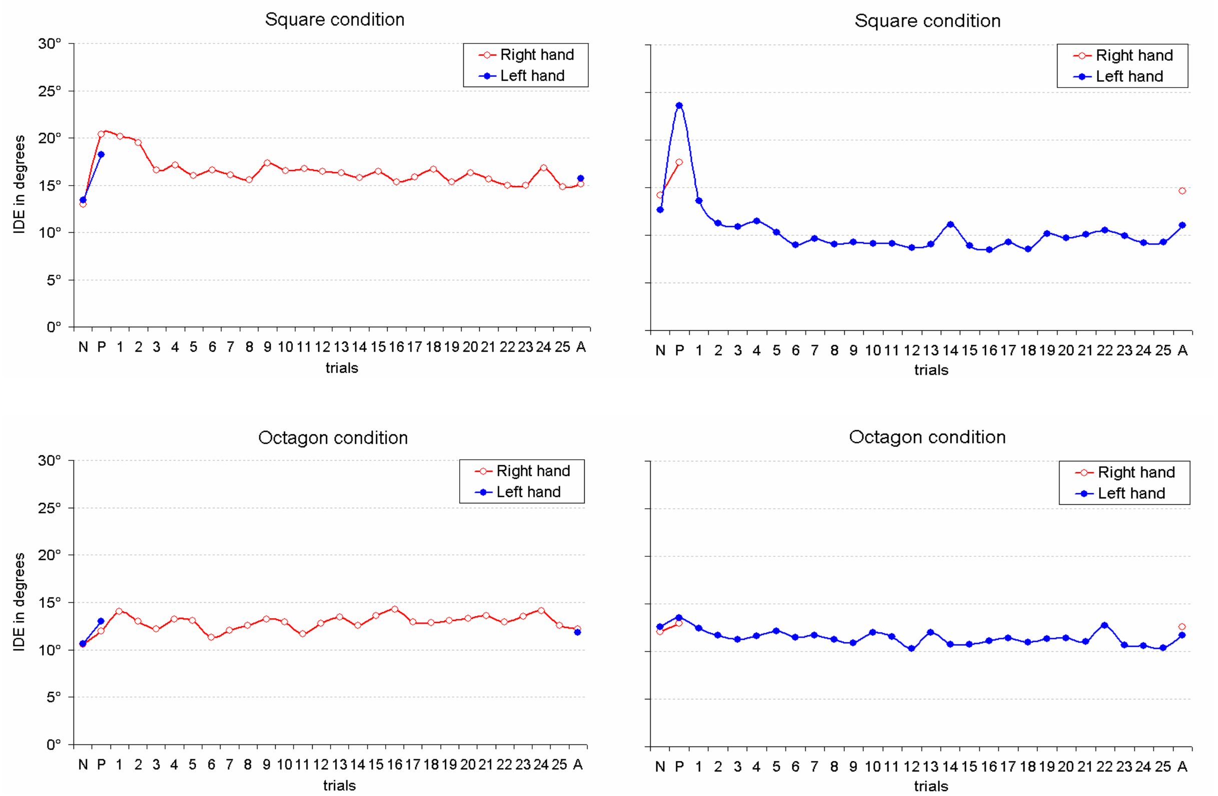


Figure 5.2 shows right and left hand IDE performance per trial-type (averaged across conditions and participants). The graphs on the left side show performance on the different trial-types for the Right-hand trained group. N.B. participants performed naïve, pre-adapted and adapted tests with both hands, but they were only allowed to use the right hand during adaptation training. The graphs on the right side show performance of the Left-hand trained group.

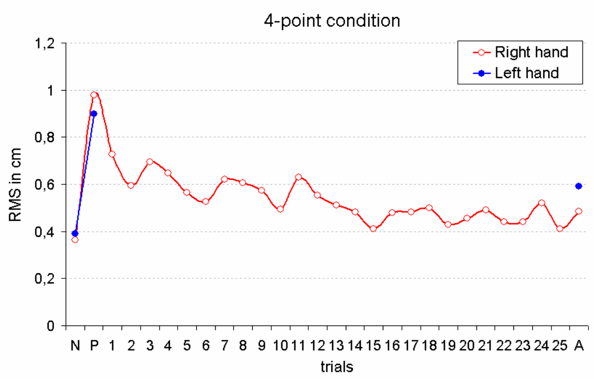
5.3.2 Root Mean Square Error

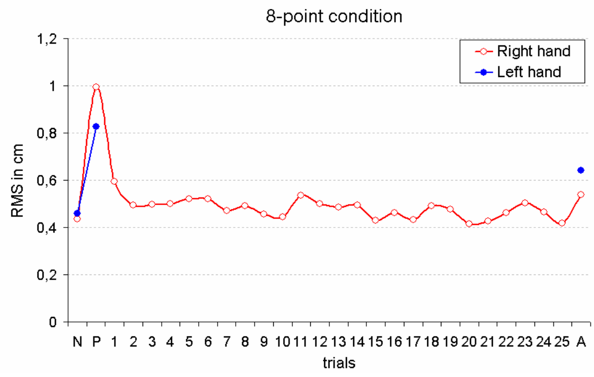
Comparing the accuracy of the right-hand trained and left-hand trained groups revealed a main effect of training ($F_{(2,95)} = 232.116$, p<.001) as well as for trial-type ($F_{(5,92)} = 120.207$, p<.001) and condition ($F_{(5,96)} = 5.515$, p< .001). The training effect showed the ‘normal’ curve, with an accuracy error increase at distortion onset for all trial-types, followed by the gradual decrease throughout training with accuracy returning to or close to undistorted baseline levels. No significant effects were found for group (right- versus left-trained) and hand (right versus left).

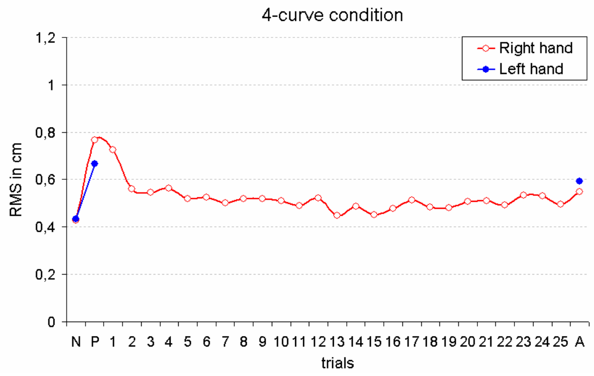
Figure 5.3 shows the intermanual effects for the root mean square error for both groups, per condition. The right-trained group showed a main effect of training ($F_{(2,47)} = 92.065$, p< .001) as well as a main effect of trial-type ($F_{(5,44)} = F = 53.321$, p< .001) and condition ($F_{(5,48)} = 4.376$, p< .01). The left-trained group also showed effects of training ($F_{(2,47)} = 161.893$, p< .001), trial-type ($F_{(5,44)} = F = 72.612$, p< .001) and condition ($F_{(5,48)} = 5.156$, p< .01).

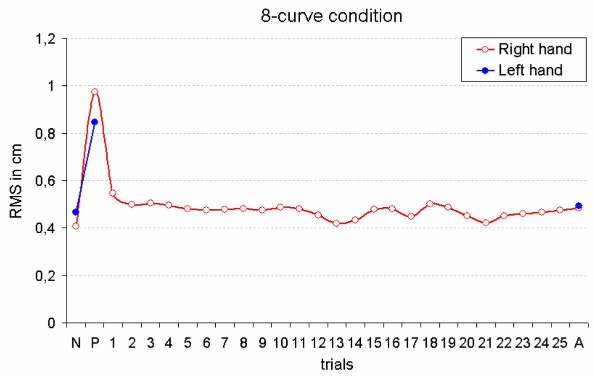
Right and Left hand RMS Performance per Trial-type

Trained with Right hand

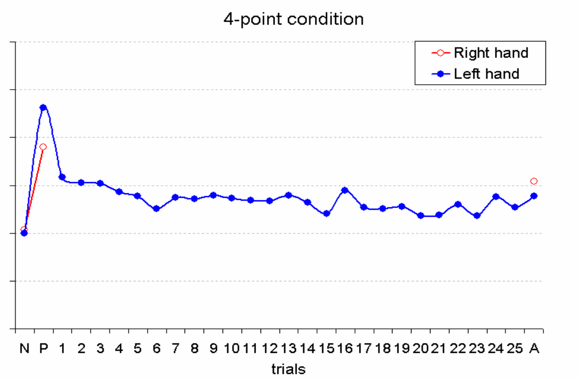


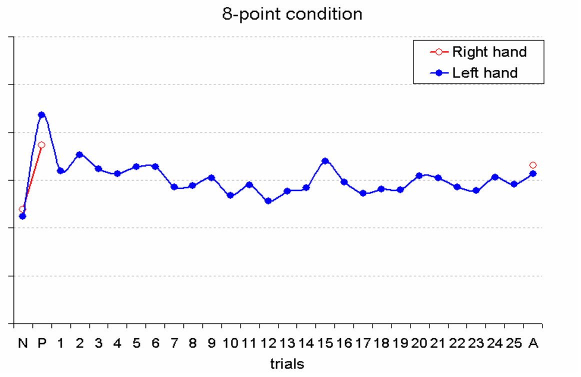


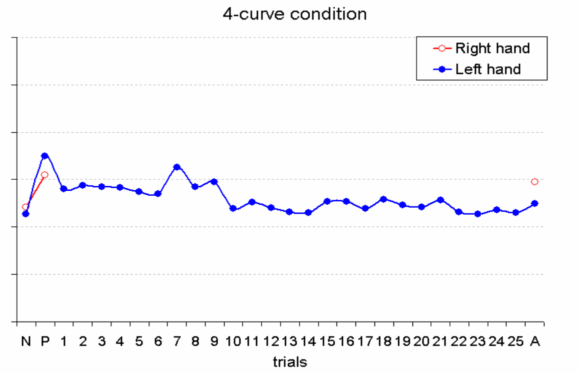


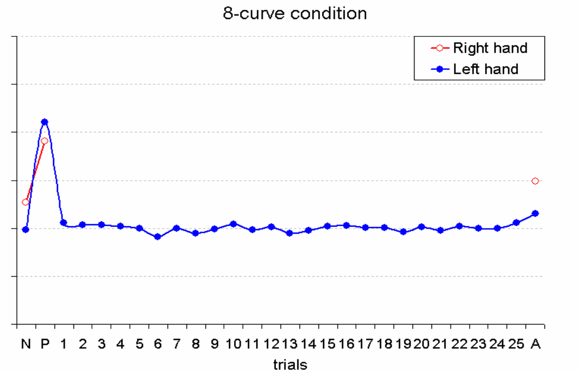


Trained with Left hand









Right and Left hand RMS Performance per Trial-type (Continued)

Trained with Right hand **Trained with Left hand**

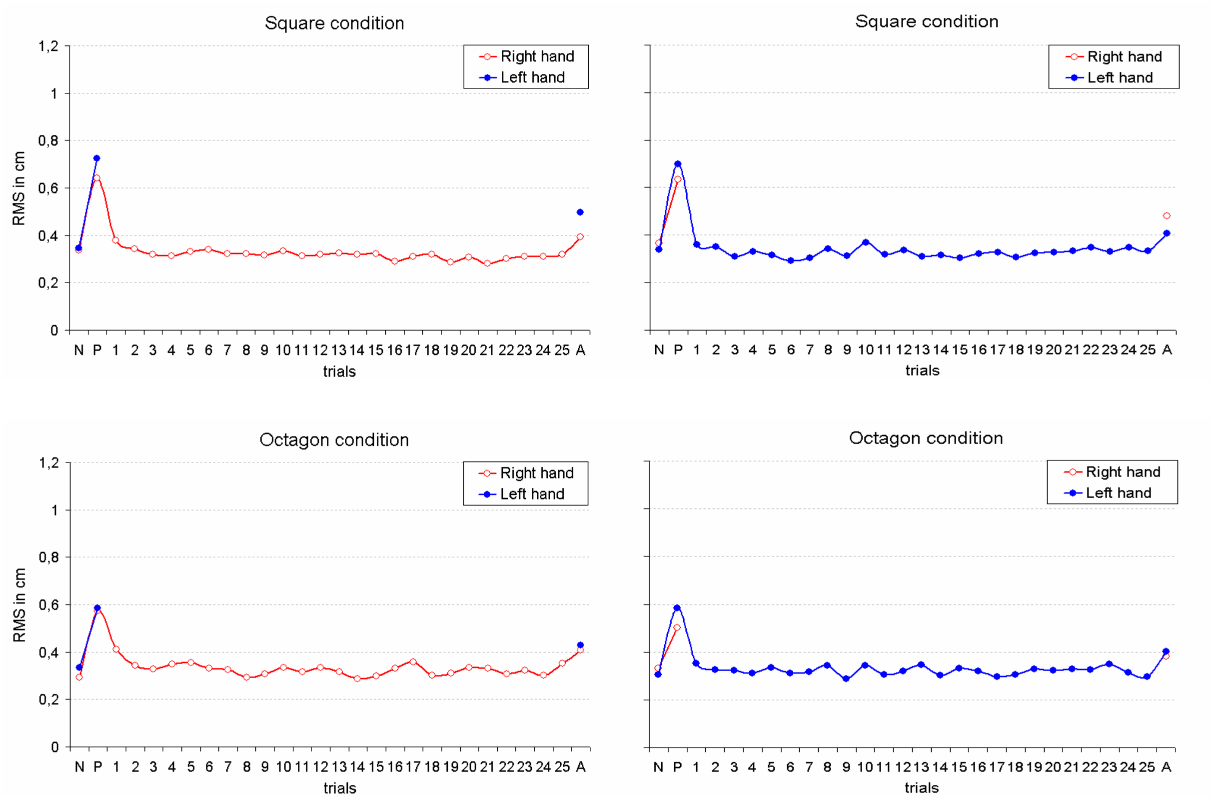


Figure 5.3 shows right and left hand RMS performance per trial-type (averaged across conditions and participants). The graphs on the left side show performance on the different trial-types for the Right-hand trained group. N.B. participants performed naïve, pre-adapted and adapted tests with both hands, but they were only allowed to use the right hand during adaptation training. The graphs on the right side show performance of the Left-hand trained group.

5.4 *Discussion and Conclusion*

The current experiment studied intermanual transfer on a visuomotor task with a 45° rotation distortion, measuring participants their initial direction errors as well as their root mean square errors. Participants performed two center-out and four tracing tasks of which two were polygon shapes and two were continuous shapes. I measured performance of both hands on two baselines, the first without the rotation distortion (naïve) and the second with a distortion (pre-adapted) then participants were trained on one hand only (right-trained or left-trained group) and finally they performed another set of test-trials with both hands. Results revealed that there was no preference for hand used or hand trained, meaning participants showed no significant differences in performance for the right or the left hand. In addition, when trained on the right hand, there was positive transfer from the right to the left hand. Similarly, there was a positive transfer from the left to the right hand when trained on the left hand.

The current findings support the hypothesis that each arm controller has access to information learned during opposite arm training. Motor control is often assumed to have a hierarchical organization with an abstract effector-independent level constraining lower effector-dependent levels (Rosenbaum, Kenny, & Derr, 1983; Van Mier & Hulstijn, 1993; Tresilian, 1999). This means that the CNS contains an abstract representation of the movement and a basic movement plan, similar to the previously mentioned internal models. Additionally, this common description is abstract in such a way that the movement can be executed with different effectors (e.g. right versus left hand) or different muscles of the same effector (e.g. right hand versus right arm). In reference to effector independence, the handwriting study by Raibert (1977) is often cited as empirical support of an abstract representation. In his study, Raibert wrote the same sentence with different effectors. He found that regardless of the effector used (right hand, right arm, left hand, mouth or foot) the overall pattern of handwriting was the same. The shape of the letters was invariant in all writing conditions. Wright (1990), however, showed that although the overall shape of the letters was very similar, marked differences between effectors were apparent, indicating a certain level of effector dependency as well.

If such an internal model or abstract representation exists, Miall and colleagues (1993) suggested that it would most likely be located in the cerebellum. In a PET study by van Mier, Tempel, Perlmutter, Raichle and Petersen (1998), participants traced cut-out maze designs with their eyes closed. Interestingly a switch in brain activity was observed from unskilled to skilled performance. During naïve or unskilled performance, most activation was found in the premotor and parietal regions as well as the cerebellum whereas during skilled performance most activation was in the supplementary motor area (SMA). The premotor and supplementary motor cortices are specialized for skilled voluntary movements. SMA is responsible for planning and coordination of complex movements, innervating distal motor units, such as fingers and toes, whereas PMA is responsible for sensory guidance of movement and control of proximal motor units, such as arms, legs, and the trunk. This leaves the cerebellum to be the most likely structure for the abstract representation (or internal model) of a movement.

The current results confirm findings from other studies with symmetrical transfer on a visuomotor rotation task (Sainburg & Wang, 2002) or on a maze tracing (van Mier et al., 1998; van Mier & Petersen, 2006). In addition, the current findings support the hypothesis that each arm controller has access to information learned during opposite arm training, since performance of both hands was similar regardless of whether participants trained with their right or their left hand. The same unambiguous (symmetrical) intermanual transfer has been shown in a study by Sainburg & Wang (2002) using a visuomotor rotation task as well. Additionally, they found that different features transferred differently across the arms, suggesting that each effector uses the 'general' knowledge differently, perhaps for particular features of a movement. Savin & Morton (2007) also found a broad generalization when adapting participants to a prism rotation while walking; they were able to point correctly under the same rotated prism distortion, hereby transferring the walking knowledge to the pointing task. These studies provide a somewhat clouded picture, on one hand there is a broad generalization whereas on the other there is a very specific transfer of only limited features across the hands. The current study tried to examine the boundaries of this intermanual transfer by testing both hands on a series of different movement categories. The results showed that left and right hand performance prior to practice was similar indicating that participants can perform the task equally well with either hand, making a direct comparison between hands more reliable. In addition, performance was measured across different movement categories. Participants performed well on the discrete center-out movements, with a large increase at distortion onset and a gradual decrease throughout training. Again, performance for left and right hand was similar across the groups. Performance on the square was similar to center-out movements as expected from discontinuous movements. In contrast, performance on the 4-curve, 8-curve and the octagon did not show a large error increase at distortion onset. Moreover, training on the 8-point trial did not have an effect on intermanual transfer (Wang & Sainburg, 2004). Concluding, intermanual transfer is symmetrical across hands. Similar to earlier results, movement categories influence the level of performance. The rotation distortion has a rather large influence on center-out and discontinuous movements, whereas the influence on continuous movements (and the octagon) was negligible.

CONCLUSION

The focus of this dissertation was on the adaptation to a visuomotor rotation and its generalization across different movement categories (discrete, discontinuous and continuous). The task involved motor planning, task demands as well as incorporating aspects such as the starting point and the direction in which to proceed, or the point where the direction of the line must be changed, the angle or curve used when changing directions. Participants were required to perform movements in three movement categories: (1) discrete movements, (2) discontinuous movements (e.g. triangle, square, hexagon and octagon) and (3) continuous movements (e.g. 4-curved star, 8-curved star and a circle). The movements were performed under normal and distorted feedback conditions, using a 45° rotation distortion of the visual feedback. Participants (pre-)planning was measured by the initial direction errors (IDE) at movement onset, their accuracy and online control through means of the Root Mean Square Error (RMS), and their movement speed by the mean movement velocity (VEL).

Overall, the results showed that performance was very good under normal (undistorted) conditions, using a stylus pen and a writing tablet did not limit performance. The first exposure to the rotation distortion had a large effect on the discrete movements. The rotated feedback disrupted both planning and accuracy performance severely. The discontinuous movements showed a mixed effect. The triangle and square showed a large error increase for both planning (IDE) and accuracy (RMS), whereas the hexagon and octagon showed only a small loss in accuracy but none in planning. Finally, the continuous movements showed only error increases for accuracy but none for direction errors. In brief, results showed that the more complex the movement[8] (or the more continuous) the smaller the disrupting effect of the rotation distortion. The hypothesis put forward and confirmed was that easier movements are planned as a whole before movement execution (feed-forward), whereas more complex movements only use a basic plan and rely more on the visual feedback during movement execution. I investigated this latter idea in the third experiment (chapter 4), where the visual target disappeared. Theories of visual guidance, commonly describe the mechanism of visual feedback as an ‘error detection mechanism’. The motor system notices a deviation from the

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[8] The movement continuum starts with the easy discrete movements, to the moderate discontinuous movements and ends with the complex continuous movements (Schmidt & Lee, 1999; 2005).

actual movement and the expected or planned movement towards the target. It then tries to minimize this error and continuously checks the deviation error. Hence, I was interested in what would occur if the reference i.e. the target location or shape was removed. Participants would no longer be able to compare their performed movements with the actual target, thus visual feedback would become more or less irrelevant or at least non-informative. The results suggested that participants used something like an internal model or movement plan to execute the movement, not having or needing to rely on visual feedback made drawing a circle very easy. It was harder for those participants who were still able to see the reference target. Interestingly, the discrete movements did not show any change influenced by the removal of the target. This reconfirms that participants most likely do not use any feedback while drawing a line, and solely rely on feed-forward mechanisms.

The final study, focused on a slightly different area in movement learning and generalization. I investigated generalization across different effectors i.e. intermanual interference. The aim was to discover intermanual transfer effects on the same tasks of discrete, discontinuous and continuous movements. Interestingly, the effect of transfer was of a symmetrical nature, meaning that the transfer from the right to the untrained left hand was just as large as the transfer from the left to the right hand.

I concluded from the results that learning a motor task is best described by a hybrid model, which incorporates both feedback and feed-forward components. As the increase of direction errors show, a crude a priori plan of the movement is established before movement onset. This movement plan is probably derived from some sort of an internal model of this movement, based upon prior experiences. During this initial movement period, no feedback mechanisms (can) influence movement execution. However, shortly after (after about 200 ms.) feedback loops are active, since participants correct their movement paths in accordance with the rotation distortion. These feedback loops allow an updating of the current movement through both a feed-forward model correcting the online movement as well as by updating the internal model with the new movement parameters. The most likely candidate to accomplish this task is probably the cerebellum, evidence from other studies supports this but more evidence needs to be provided. Additionally, all studies presented and discussed here are in one way or another, a measure of skill transfer either across movement categories or across hands. In general, transfer of learning refers to the gain or loss in proficiency on a motor task with a particular limb as the result of practice with a different or contralateral limb on the same motor task, without any prior involvement of the latter during task acquisition. The studies described here showed that there was a substantial amount of transfer.

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CURRICULUM VITAE

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Basic and Vocational Education

1991 – 1996	High School degree ‘Bernardinus College’, Heerlen, the Netherlands
1997 – 1998	Propedeutical exam Creative Therapy (60 ECTS), Hogeschool Zuyd, Sittard

University Education

1999 – 2004	MSc. In Biological Psychology, University of Maastricht, the Netherlands Majors: Developmental Psychology and Neurocognition
2003 – 2004	Research Internship and Lab Assistant, Prof. E. Thelen’s Infant Motor Lab, Indiana University, Bloomington, Indiana, USA
2004 – 2007	Ph.D. student at the International Graduate School of Neuroscience, Ruhr University Bochum, Germany

Teaching Experience

1996 – 1997	Teaching Assistant, AFNORTH, International School
1994 – 2001	Classical Ballet teacher, Ballet school Charlotte van Rooijen (NL)
2001 – 2002	Classical Ballet teacher, Ballet school Chantalle (NL)
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Publications

Otte, E., & van Mier, H.I. (2006). Bimanual interference in children performing a dual motor task. Human Movement Science, 25, 678–693.

Selected Conference Abstracts

Otte, E. & van Mier, H.I. (2005). Development of Bimanual Coordination in 4 to 11-year-old Children. International Graphonomics Society, Salerno, Italy, 26-29 June 2005.

Otte, E., Hoffmann, K-P., & Würtz, R.P. (2005). Transfer of adaptation across movement categories: from point-to-point movements to tracing figures. Summer School Perception & Action, Seeon, Germany, 15-19 August 2005.

Otte, E., & Thelen, E. (2006). Stability and Perseveration of Looking during a Looking, Kicking and Reaching A-not-B task. European Science Foundation: Brain Development and Cognition in human Infants, Acquafredda di Maratea, Italy. 1-6 October 2005.

Otte, E., & Thelen, E. (2006). Stability and Perseveration of Looking during a Looking, Kicking and Reaching A-not-B task. International Conference on Development and Learning, Bloomington, IN, USA. 31 May - 3 June 2006.

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Awards

Best Graduate Student Presentation Award – International Graphonomics Society, Salerno, Italy, 2005. Development of Bimanual Coordination in 4-11 year old children.