Cognitive Planning in Manual Action

Action selection in multi-segment object manipulation tasks

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Bielefeld, April 2014 Christian Seegelke

To my father († 2011)

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Chapter 3

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Chapter 4

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Contents

1 General Introduction

1.1 Perceptual-motor integration problem

Strictly speaking, movement provides the only means by which humans not only physically interact with the world, but also actively operate on this world. In more dramatic language, ”from the motor chauvinist’s point of view the entire purpose of the human brain is to produce movement” (Wolpert, Ghahramani, & Flanagan, 2001, p. 487), and all sensory and cognitive processes can be regarded as inputs for future motor outputs (Bernstein, 1967; Wolpert et al., 2001). Consequently, the human motor system is vital to the understanding of basic processes underlying any kind of (inter-) action with the sensory environment. Although there is growing consensus that sensory and motor processes are tightly interconnected, one of the core problem in motor control research is precisely how perception and motor control are combined (Rosenbaum, 2010).

The empirical work of the present thesis is concerned with how the motor system plans and controls manual actions during multi-segment action sequences involving object manipulation. Consequently, work on the perceptual-motor integration problem, which is presented in the following, is of high relevance to this thesis.

1.1.1 Woodworth’s pioneering work

Early work on perceptual-motor control was conducted by Woodworth at the end of the 19th century. In his now seminal paper *‘The accuracy of voluntary movement’*, Woodworth (1899) provided a number of valuable contributions to the understanding of perception and motor control, upon which current models still build (see Elliott et al., 2010; Elliott, Helsen, & Chua, 2001, for reviews). In these experiments, Woodworth (1899) had participants perform back-and-forth (i.e., reciprocal) aiming movements with a pencil on paper either between two lines of fixed distance, or such that the amplitude of the current movement matched the amplitude of the previous movement. The paper was secured to a drum rotating at constant speed which allowed Woodworth to measure the spatial accuracy of a movement (i.e., endpoint error), as well as the spatiotemporal characteristics of the movement trajectory. Woodworth noticed that the initial phase of the movement was relatively rapid and stereotyped. In contrast, as the pen approached the target, the movements slowed down, the trajectories revealed discontinuities, and variability increased. Based on these findings, he proposed a model which has come to be known as the *two-component model of goal-directed aiming*. This model holds that aiming movements are comprised of an initial impulse phase followed by a current control phase. The initial impulse phase is thought to be centrally preprogrammed (i.e., open-loop) and acts to propel the limb towards the target. In the subsequent current control phase, sensory feedback is utilized to make necessary adjustments to the movement that causes the limb to 'home in' on the target (i.e., closed-loop).

To examine the contribution of sensory (i.e., visual) feedback on the relation between the accuracy and the speed of goal-directed aiming movements, the movements in Woodworth's experiments were performed in time with a metronome set at rates between 20 and 200 strokes per minute in steps of 20 strokes per minute (i.e., movement times between 300 ms and 3000 ms, step rate = 300 ms), and either with the eyes open or the eyes closed. During the eyes-closed condition, spatial accuracy was relatively similar regardless of movement speed. In contrast, during the eyes-open condition, spatial error increased with movement speeds up to between 120 to 160 metronome strokes per minute (depending on which hand was used) which corresponds to an average movement duration of about 450 ms. Further increases in movement speed did not lead to larger errors, and it was also at this speed where the error in the eyes-open condition approached the error in the eyes-closed condition. From these results Woodworth inferred the processing time for visual feedback to be approximately 450 ms.

Although Woodworth's theoretical and empirical contributions can certainly be considered as milestones in motor control research, the method to determine the time to use visual feedback was error-prone. As participants in Woodworth's experiments performed reciprocal movements, the duration of each movement not only included the time to bring the limb to the target, but also the time required to reverse the movement once the target was hit (Elliott et al., 2010, 2001; Keele & Posner, 1968). Consequently, the proposed value of about 450 ms to process visual feedback was likely an overestimation.

By using discrete, rather than reciprocal, aiming movements, Keele and Posner (1968) reduced Woodworth's estimate by about half. Participants performed movements of 190 ms, 260 ms, 350 ms, and 450 ms duration. In half of the trials, room lights were randomly extinguished upon movement initiation. Results showed that during the slow movement conditions (i.e., durations of 260 ms, 350 ms, and 450 ms) participants performed more accurately (i.e., less target misses) when vision was available. However, during the 190 ms condition (fast movement condition), there was no difference in performance accuracy between the light-on and lights-off condition. Thus, Keele and Posner (1968) concluded that the minimum duration for processing visual feedback from a movement appears to be between 190 ms and 260 ms.

Later research even further reduced this suggested estimate (Zelaznik, Hawkins, & Kisselburgh, 1983). In the experiments of Keele and Posner (1968) the lights went off unpredictably, and as such it was reasoned that uncertainty about the availability of visual feedback might have affected participants' movements. In other words, if participants were given advance knowledge about whether or not visual feedback is available, they could prepare their movement adequately. Zelaznik et al. (1983) modified the paradigm of Keele and Posner (1968) by blocking vision and no-vision trials, such that participants always had certainty about visual feedback availability. In doing so, Zelaznik et al. (1983) showed clear accuracy differences between vision and no-vision trials for movement times of 150 ms (no differences in accuracy were found for movement times of 75 ms). In sum, the research presented above provides compelling evidence for the tremendous influence of sensory information when it comes to error correction in goal-directed aiming, even when the movements are performed very rapidly.

1.1.2 Feedback and feedforward control

Error correction based on sensory feedback is possible via feedback loops (see Figure 1.1). Bringing the hand to a target can be taken as an illustrative example (Rosenbaum, 2010). First, a reference signal is entered into the loop which provides information about the goal state to be achieved (e.g., a representation of the hand at the target). Subsequently, the plant (i.e., the body part being controlled) converts the input signals into output (e.g., moving the hand towards the target). Finally, the comparator measures the discrepancy between the actual position of the hand and the intended position of the hand, and uses this information to negate feedback (i.e., closed-loop control).

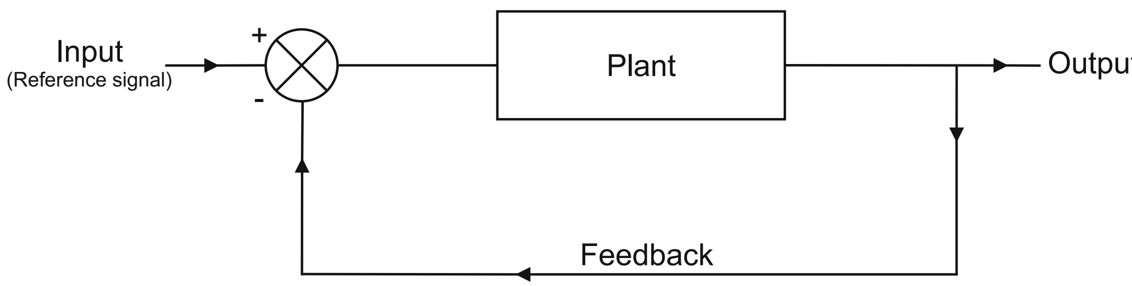

Figure 1.1: Feedback loop. Adapted from Legge and Barber (1976)

Nevertheless, there is evidence that movements can be performed reasonably well even in the absence of sensory feedback (i.e., open-loop control). In animals, deprivation of (somato-)sensory feedback is achieved by severing the nerve fibers that transmit sensory signals from the limbs to the spinal cord (Knapp, Taub, & Berman, 1963). It has been demonstrated that monkeys with deafferented forelimbs are still able to point accurately to visual targets, even if the responding limb was occluded (Taub & Berman, 1968; Taub, Goldberg, & Taub, 1975). However, pointing accuracy was inferior compared to monkeys not lacking sensory feedback. Similar phenomena have been observed in humans. For example, Lashley (1917) reported that the control of the movements of a man who suffered from anaesthetic legs (due to a gunshot wound of the spinal cord) were comparable to that of a healthy individual. Similarly, Rothwell et al. (1982) demonstrated that a man deafferented due to a sensory neuropathy was able to perform a variety of manual movements, such as touching his thumb with each finger, tapping, or drawing different shapes and figures in the air, with remarkable accuracy (see also Marsden, Rothwell, & Day, 1984).

These findings indicate that movements are not only controlled via feedback mechanisms, but also by generating predictive models about the motor outcomes (i.e., feedforward control). Feedforward mechanisms enable the central nervous system to distinguish between perceptual changes evoked by one's own movement and perceptual changes caused by motion in the external environment. This disambiguation is achieved by an internal subtraction process which was first acknowledged by Helmholtz (1867) and has become known as the reafference principle (von Holst & Mittelstaedt, 1950, see Figure 1.2). Specifically, it was proposed that when producing a motor command (efference), the motor system generates an internal copy of this signal (efference copy) which encodes sensory information of the movement (reafference). The efference copy can then be subtracted from the sensory input (afference) leaving only sensory input from outside influences (exafference). Compelling evidence for this principle was obtained from an experiment with flies (von Holst & Mittelstaedt, 1950), but similar mechanisms have also been found in humans (Sperry, 1950; Wolpert & Flanagan, 2001). In sum, these findings demonstrate that both feedback and feedforward mechanisms play a considerable role in the control of human movement and that the sensorimotor system generates predictive (or anticipative) models that encode the sensory consequences of the motor outcomes.

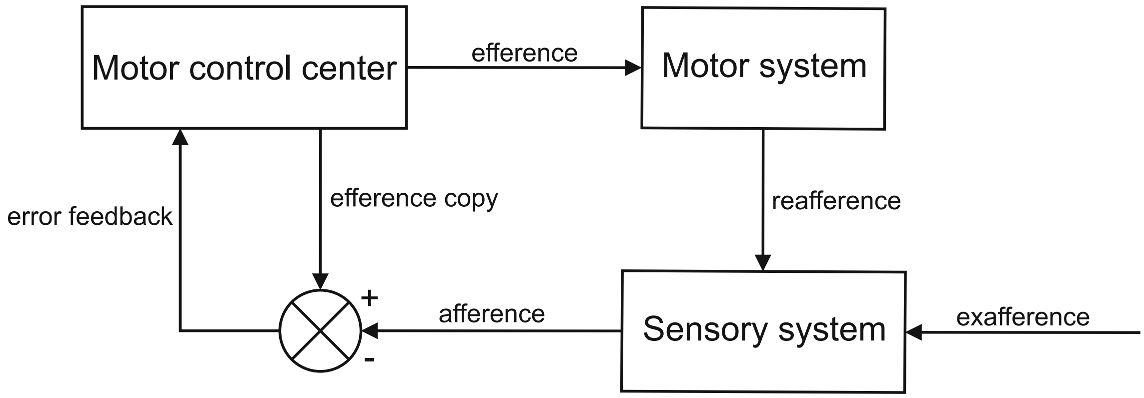

Figure 1.2: Reafference principle. Adapted from von Holst and Mittelstaedt (1950)

1.1.3 The role of sensory effects in action planning

The idea that actions are guided by the anticipation of perceptual effects was not only addressed by physiologists (e.g., von Holst & Mittelstaedt, 1950), but also by researchers in the field of psychology (Herbart, 1825; James, 1890; Lotze, 1852). Furthermore, the basic principles remain highly relevant to current theoretical conceptions in cognitive psychology such as the ideomotor approach (Knuf, Aschersleben, & Prinz, 2001), the common-coding approach (Prinz, 1997), the theory of event coding (Hommel, Müsseler, Aschersleben, & Prinz, 2001), and the anticipative behavioral control approach (Hoffmann, 1993). These aforementioned perspectives all share the belief that actions are represented in terms of anticipated features of the intended goal. That is, in terms of the intended effect they aim to achieve.

Various experiments have provided empirical in support of this view (see Hommel, 2003, 2009; Kunde, 2006; Schütz-Bosbach & Prinz, 2007, for reviews), work on response-effect compatibility being one branch in this context. In these tasks, it has been demonstrated that participants' motor responses are facilitated if the required response is followed by a compatible as opposed to an incompatible sensory effect (e.g., Kunde, 2001, 2003; Kunde, Koch, & Hoffmann, 2004). For example, a forceful key press is initiated faster if it is reliably followed by a loud auditory tone as compared to a quiet tone, whereas this pattern is reversed for a soft key press (Kunde, 2001). Similarly, Mechsner, Kerzel, Knoblich, and Prinz (2001) have shown that the symmetry bias in the production of bimanual movements is towards spatial, perceptual symmetry rather muscular symmetry, lending further support to the assumption that human movements are organized based on sensory effect representations.

Interestingly, the idea that sensory information plays a crucial role in the control of voluntary movement was noted in the pioneering work of Bernstein in the field of movement science. Typically, human motor behavior seeks to achieve action goals related to the environment. Hence, given a certain action goal, the motor system's task is to generate a movement that will attain this goal, and hence, bring about a change in the sensory environment (van Soest & van Ingen Schenau, 1998). Bernstein (1967) acknowledged the important role of sensory feedback processing in the control of voluntary movements, and pointed out the goal-directed character of motor acts. This idea is reflected in his scheme of motor control based on goal definition and error correction (Bernstein, 1967) and is reminiscent to that of von Holst and Mittelstaedt (1950). Bernstein (1967) explicitly emphasized the importance of anticipation in realizing any type of goal-directed motor act, and that any voluntary motor action cannot be initiated without a model of what should result from the planned action. This idea is expressed in his *model of the desired a future* (i.e., a model of what should be) which is supposed to play an important role in controlling motor acts. He stated that

> in a similar way to that in which the brain forms an image of the real external world – an image of the factual situation at a given moment, and of situations which have been experienced in the past of which we have impressions in our memory – it must possess to some degree the capacity to form a representation of (or, what is the essence of the matter, to plan in advance) situations which are as yet unrealized, and which the biological requirements of the organism impel it to realize

(Bernstein, 1967, p. 150).

A model of the future must therefore be qualitatively quite different to models of the past and the present – which are unambiguous and categorical – as it can only be based on extrapolation with a certain probability. Such a probabilistic prognosis is contingent upon memory of past events and the perception of present events. The challenge for the motor system is to create an appropriate model of the future that contains the necessary information to generate motor commands that transform the current state in the sensory environment into the desired state, and hence accomplish the intended action goal.

1.2 Motor equivalence and the degrees of freedom problem

After having considered the problem of how perceptual and motor processes are integrated, the attention will now be drawn to another central problem in motor control research. American neurophysiologist Karl Lashley was one of the first who noted that the motor system is capable of achieving the same goal by different means, a phenomenon termed motor equivalence (Lashley, 1930, 1933). In other words, different motor commands may lead to the same change in the sensory environment. Lashley gained initial evidence for this principle from behavioral experiments in rats and monkeys (Lashley, 1924, 1930; Lashley & McCarthy, 1926). In the former, Lashley and McCarthy (1926) trained rats in a rectangular maze and observed their subsequent errorless running. The authors noted that the same individual followed the correct path, and hence accomplished the task goal, by using a variety of different locomotion techniques on successive trials, even after partial or complete destruction of the cerebellum. In the latter, monkeys performed manipulation tasks in which they had to open problem boxes to retrieve food reward (Lashley, 1924). After destruction of precentral motor areas, the monkeys showed adaptive changes in behavior still allowing them to achieve the task goal despite paretic deficits.

Arguably however, the classical and most prevalent example for motor equivalence comes from hand writing (e.g., Lashley, 1933, 1942). Here, it is still possible to recognize an individual's handwriting regardless of the effector with which it was produced. Thus, independent of whether one uses the dominant or non-dominant hand, the feet or even the teeth, the characteristic style of one's handwriting is preserved. In Lashley's words:

> The shift from writing with finger movements to movements of the arm or even with a pencil held in the teeth still preserves the characteristics of individual chirography. Of course there are limits to such transfers which are set by the fineness and accuracy of the movements involved, but the essential patterns may be imposed upon the muscles of any limb (Lashley, 1933, p. 25).

Later research has further confirmed the invariance of written script across different effectors (Castiello & Stelmach, 1993; Keele, 1981; Wright, 1990), changes in writing time and size (Wright, 1993), and the orientation of the writing surface (Merton, 1972).

Motor equivalence is closely related to the degrees of freedom problem, formulated by the Russian neurophysiologist Nikolai Bernstein (e.g., Bernstein, 1967). The degrees of freedom problem states that there is an infinite number of ways in which a movement can be performed in order to achieve the same action goal. This is due to the fact that the motor system has redundant anatomical, kinematic, and neurophysiological degrees of freedom. A given motor task can be realized through different joint configurations. A given joint configuration can be achieved with different paths, and each path can be performed with different velocities. Furthermore, this can be achieved through different muscle activation patterns and any given muscle activation pattern can be achieved with many different patterns of neural activation. Consequently, there exists no unequivocal relationship between a motor problem (or task) and a solution to this problem. Bernstein reasoned that stored motor engrams in CNS (i.e., a memory structure) must exist, which transform an abstract code into an action sequence. Furthermore, he concluded that engrams do not include any metric projections of joints and muscles, but rather a general projection of external space representing the final motor output. According to Bernstein, motor coordination ”is the process of mastering redundant degrees of freedom of the moving organ, in other words, its conversion to a controllable system” (1967, p. 127).

1.3 Approaches to the degrees of freedom problem

Bernstein pursued two approaches to address the degrees of freedom problem. The first is embedded in the concept of synergies, that is, to identify functional dependencies or interactions between effectors. The idea was that linkages between effectors could effectively reduce the number of degrees of freedom that must be independently controlled. As early as 1939, von Holst observed the presence of such couplings in fish and humans (von Holst, 1939). Specifically, he noted that the oscillation of a fish’s dorsal fin changes when the right and left pectoral fins start to oscillate. Similarly, oscillating the right arm at increasing frequencies in human participants affects the oscillations of the left arm. Such synergies have been studied in detail between limbs (Swinnen, Heuer, & Casaer, 1994), but they also occur within a limb (e.g., d’Avella & Lacquaniti, 2013; d’Avella, Portone, Fernandez, & Lacquaniti, 2006; Kots & Syrovegnin, 1966). For example, d’Avella et al. (2006) demonstrated that four to five muscle synergies captured most of the variance when performing fast-reaching movements between a central location and peripheral targets. Synergies certainly bias the neuro-motor system to act in specific ways (and thus reduce the numbers of degrees of freedom to be independently controlled), but they do not obviate the degrees of freedom problem. It is certainly more natural and easier to flex the elbow while also flexing the wrist and extending the elbow while extending the wrist rather than the other way around (i.e., flexing the elbow while extending the wrist and vice versa). Nevertheless, it is still possible to execute the latter task, though with greater difficulty. Thus, synergies are not fixed but strongly depend on the task to be achieved, and hence do not fully solve the degrees of freedom problem.

The second approach pursued by Bernstein concerned the exploitation of mechanics. The idea is that exploiting mechanical interactions between the body and the environment eliminates the need to control each feature of action control. This can be illustrated by the example of walking. A typical human walking cycle is comprised of two phases for a given leg. During the stance phase the foot has contact to the ground. During the swing phase the leg is brought forward. It has been shown that during the swing phase there is virtually no muscle activation. The swing is completed by virtue of gravity. Consequently, this phase does not need to be planned and controlled in detail. Exploitation of mechanics during walking has also been successfully applied in the field of robotics in the so-called *passive dynamic walkers* (Collins, Ruina, Tedrake, & Wisse, 2005). These mechanical devices need hardly any control to resemble people's gait pattern, at least in controlled environments. However, this approach is limited in a sense that it cannot explain many voluntary initiated actions.

A third approach, which came up after Bernstein, aims at elucidating factors that consistently influence action selection. The idea is that movements that are (more often) performed are in some way more efficient than movements that are not or less often performed. These factors are commonly referred to as efficiency constraints of action selection (Rosenbaum, 2010; Rosenbaum, Chapman, Coelho, Gong, & Studenka, 2013). As constraints limit the range of possible actions, the core challenge for researchers is to identify these constraints. Several of such constraints have been proposed based on examination of reaching movements. For example, participants tend to move their hand in straight lines (Abend, Bizzi, & Morasso, 1982; Hollerbach, Moore, & Atkeson, 1987; Morasso, 1981) and with a smooth, bell-shaped velocity profile (Flash & Hogan, 1985) which reaches its peak near the midpoint of displacement (Abend et al., 1982; Cooke, 1980). From the viewpoint of optimization theory (Jordan & Wolpert, 1999; Todorov, 2004; Todorov & Jordan, 2002) the central nervous system seeks to minimize a certain cost associated with the movement. Several criteria or variables that might be optimized have been put forward, such as minimizing the mean squared rate of change of acceleration over movement time (i.e., minimum jerk principle, Hogan, 1984; Hogan & Flash, 1987), minimizing end-point variance (Harris & Wolpert, 1998), or minimizing torque change (Uno, Kawato, & Suzuki, 1989). However, variables to be optimized may vary depending on the task to be executed. Whereas some constraints might be highly important in one task, they might be less important in another. Consequently, action selection involves the process of determining a ranking or weighting of different constraints (Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; Rosenbaum et al., 2013; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; Seegelke, Hughes, & Schack, 2011; van der Wel & Rosenbaum, 2010).

1.4 Hierarchical models of action control

The idea that action selection involves ranking different constraints is reflected in the posture-based motor planning model by Rosenbaum and colleagues (Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, and Engelbrecht, 1995; Rosenbaum et al., 2001). The authors argue that decision-making about movement is formally no different from any other kinds of decision-making process such as which car to buy. Similar to Tversky's (1972) elimination by aspects theory of choice, action selection might be best understood as a winnowing process, that is, ranking constraints from most to least important. Such a model achieves that all possible constraints are included in the process, but they differ with respect to their weight. The actor weighs the constraints in response to the environment. That way, the weighting of the constraints define the task to be performed as represented by the actor. Thus, the internal representation of a task is a ranking of constraints, or what is called a constraint hierarchy. Rosenbaum et al. (2001) claim that the constraints relevant for performing movements (at least for generating positioning movements) pertain to features of future body postures. Generating a movement involves first identifying a goal posture (i.e., a target position of the body), and then determining a movement that leads from the starting posture to this goal posture. The suggestion that movements and goal postures are distinguishable is supported by several empirical observations. First, people are much better in reproducing body postures they recently adopted than reproducing features of body movements that led to this postures (Marteniuk & Roy, 1972; Smyth, 1984). Second, Polit and Bizzi (1979) demonstrated that deafferented monkeys are able to accurately point to visual targets (also in the absence of vision and auditory feedback), even if their limb was mechanically perturbed at the start of the movement. These data are consistent with the equilibrium point hypothesis (Feldman & Latash, 2005) in which muscle stiffness is centrally regulated to cause muscle antagonist forces and torques to sum to zero, and which also dissociates between goal positions and movements. Third, it has been shown that position variability decreases as target positions are approached (Newell & Corcos, 1993). Forth, the finding that stimulating cells in the monkey motor- and premotor-cortex causes monkey to adopt postures that depend on where the stimulation is applied (but not on the starting posture) have been taken as evidence for a neurophysiological representation of goal postures, as opposed to muscle activation patterns (Graziano, Taylor, & Moore, 2002).

According to the theory, people choose goal postures by evaluating recently adopted stored goal postures with respect to the current constraint hierarchy. The best candidate stored goal posture may also be modified such that a potentially better goal posture is found. Once a goal posture is selected, a movement to that posture is created, a process which also relies on a constraint hierarchy. Alongside Rosenbaum's approach to action selection and execution, there are several other models that postulate that actions are controlled via hierarchically organized plans (e.g., Bernstein, 1947; Franz, 2010; Franz &

McCormick, 2010; Jeannerod, 1997; Kilner & Blakemore, 2007; Kilner, Friston, & Frith, 2007; Kilner & Frith, 2008; Lashley, 1951; Schack, 2004; Schack & Ritter, 2009).

Bernstein (1947) proposed a model of motor coordination composed of different levels which are organized hierarchically. It was likely very much influenced by the work of John Hughlings Jackson, who had previously posited that the brain has a hierarchical organization which is driven by evolutionary principles (see Franz & Gillett, 2011; Gurfinkel & Cordo, 1998). According to Bernstein's model, the motor-control system is comprised of five structural or functional levels. On the lowest level (level 1), the level of paleokinetic regulation, which regulates muscular tonus and controls quasi-static postures, actions are completely involuntary. The level of synergies (level 2) coordinates cyclical and highly learned movements and provides a perceptual reference frame for the body, which in turn serves as a starting coordinate for sensory reception and the final target of perception. The level of spatial fields (level 3) includes the perception of the space external to the body and is important for spatial orientation and perceptual object properties. The level of actions (level 4) is responsible for object-related action organization. Finally, Bernstein introduced a level of symbolic or conceptual organization (level 5) responsible for symbolic action control. Thus, Bernstein's model contains the idea of a strong interplay between motor representations, which contain the functional structure of a movement, sensory feedback, and the action goals in service of voluntary motor planning.

Schack and colleagues (Land, Volchenkov, Bläsing, & Schack, 2013; Schack, 2004; Schack & Ritter, 2009, 2013) expanded Bernstein's model by integrating cognitive components and structures, and taking into consideration findings and ideas from approaches in cognitive psychology (e.g., Hoffmann, 1993; Hommel et al., 2001; Knuf et al., 2001). Specifically, the cognitive architecture model views the functional construction of actions on the basis of a reciprocal assignment of performance-oriented regulation levels and representation levels. It is comprised of four levels, each of which is functionally autonomous, and which can be separated into regulation and representation levels according to their central tasks (see Table 1.1). The level of sensorimotor control (level I) is directly connected to the environment and induced perceptually. It is built on functional units composed of perceptual effect representations, afferent feedback, and effectors. The essential invariant value of such functional units is the representation of the movement effect. The modality-specific information representing the effect of the movement is stored on the level of sensorimotor representation (level II). The level of mental representation (level III) predominantly forms a cognitive benchmark for the level of mental control (level IV). It is organized conceptually, and is responsible for transforming the anticipated action goal into an appropriate motor program that brings about the desired outcome. Basic Action Concepts (BAC) serve as major representational units for movements in memory and are located on this level. This idea is certainly inspired by theories about how information is generally stored in memory (e.g., Hoffmann, 1986, 1993; Hoffmann & Zießler, 1982; Rosch, 1975, 1978; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). These theories holds that information is represented in terms of categories. Without categories, each object would appear to be unique, hence, no prior knowledge could the applied. Categories classify objects based on shared features. Such features can be perceptual (i.e., classification based on color or shape), but object categorization can be also based on functional equivalence. For example, though perceptually quite different, both a pencil and a piece of chalk can be used for writing, hence they might be categorized as writing tools. Consequently, object categorization might be regarded as a cognitive categorization of objects according to the functions they share in attaining an action goal (Hoffmann, 1986). Similarly, BACs serve to classify movements that have common features and will lead to the same effects. Consequently, BACs tie together the functional and sensory features of movements. The integration of sensory features refers to perceptual movement effects, which in turn links the level of mental representation (level III) with the level of sensorimotor representation (level II). The functional features are derived from action goals. This connects this level with the level of mental control (level IV). This level is induced intentionally and responsible for coding the intended movement effect into an action goal such that the goal can serve as a cognitive benchmark for further processing.

Table 1.1: Levels of action organization (adapted from Schack & Ritter, 2009)

Code	Level	Main function	Subfunction	Tools
IV	Mental control	Regulation	Volitional initation, control strategies	Symbols, strategies
III	Mental representation	Representation	Effect-oriented adjustment	Basic action concepts
II	Sensorimotor representation	Representation	Spatial-temporal adjustment	Perceptual effect representation
I	Sensorimotor control	Regulation	Automatization	Motor primitives, basic reflexes

One way to ascertain cognitive representation structures is provided by the Structural Dimensional Analyis-Motoric (SDA-M, Schack, 2012). The SDA-M procedure ascertains relational structures in a given set of concepts, and has been applied in a number of studies addressing complex action (Schack & Mechsner, 2006; Weigelt, Ahlmeyer, Lex, & Schack, 2011), manual action (Schack & Ritter, 2009), and rehabilitation (Braun et al., 2007). Importantly, this method allows for a psychometric analysis of the structures without necessitating participants to give explicit statements regarding their representation, but rather through means of knowledge-based decisions in an experimental setting. Results of these studies have demonstrated that the cognitive representation structure of voluntary movements is related to the actual motor performance. For example, the representation structure of experts reveal a hierarchically order of basic action concepts that correspond to functionally meaningful sub-movements while novices or stroke patients show unstructured patterns and exhibit greater between-subject variability (Braun et al., 2007; Schack & Mechsner, 2006; Weigelt et al., 2011). In sum, the cognitive architecture model provides a comprehensive framework for the way movements are controlled, stemming from the volitional initiation of the action to lowest level of sensorimotor control, thereby connecting mental representations with motor output.

1.5 Object manipulation

In the previous sections, basic considerations that pertain to the field of motor control in general were outlined. Given that the focus of the present thesis is on the planning of manual action sequences, the content of the following sections is dedicated to the work on manual action control in the context of object manipulation tasks.

1.5.1 Napier's work

Much of what is known about how actions are planned, selected, and controlled, and what has led to the theoretical conceptions presented so far has been explored in the context of manual actions (i.e., pointing, aiming, and reaching movements). One domain in which the links between cognition and action become particularly intriguing is grasping and manipulating objects. Pioneering work by Napier (1956) significantly advanced the study of grasping objects. Based on anatomical and functional considerations, he introduced the distinction between power and precision grips. In the former, the object is clamped between the partly flexed fingers and the palm with counter pressure applied by the thumb. In contrast, in a precision grip the object is pinched between the tips of the fingers and the opposing thumb. Although Napier (1956) admitted that certain object properties such as the shape, size, weight, texture, temperature, or wetness of an object constitute influencing factors on the type of grasp employed, he also disclosed that these factors have no general application. For example, a pen might be grasped differently depending on whether one intends to write with it or to pass it to somebody else. If it is used for writing, one will most likely grasp it close to its tip with the tip of the thumb and the opposed fingers. In contrast, if it is passed to someone else, it may be grasped more towards its end secured by the thumb on one or two fingers. Similarly, when opening a jar lid, one will initially probably employ a power grip with the palm pressed against the lid and the fingers flexed around it. Once the lid of the jar becomes loose, one will switch to a precision grip posture with only the finger tips in contact with the lid to facilitate the removal of the lid. He proposed that the predominance of either precision or power requirements of a task determines the posture to be adopted. In Napier's words:

> While it is fully recognized that the physical form of the object may in certain conditions influence the type of prehension employed it is clear that it is the nature of the intended activity that finally influences the pattern of the grip (Napier, 1956, p. 906).

In other words, the way an object is grasped is highly influenced by what an actor plans to with that object.

1.5.2 Two component model of reaching and grasping

Since Napier's seminal paper, grasping has been extensively studied using a variety of different tasks and techniques (Bennett & Castiello, 1994; Wilson, 1998; Wing, Haggard, & Flanagan, 1996). Jeannerod (1981, 1984) was the first to provide a kinematic description of human reach-to-grasp movements. He proposed that reaching and grasping an object is composed of two components – a transport component and a grasp component. The transport component is responsible for bringing the hand toward the object. The grasp component is responsible for shaping the fingers in anticipation of the grasp. These components are thought to be controlled by two independent visuomotor channels. One channel mainly processes information about intrinsic object properties. These properties such as size, mass, shape, and color of an object are independent of the object-environment relationship. The grasp component relies on information processes of this channel. The other channel processes extrinsic object properties such as position or orientation of an object relative to its environment. This information is thought to affect only the transport component.

One potential reason of why this model has been (and still is) so attractive is that the two component correspond to distinct at the level of joints, muscles, and corticospinal connections (Brinkman & Kuypers, 1973). For example, finger movements are achieved by activation of distal muscles whose motoneurons receive input from corticospinal projections (grasp component). In contrast, the hand is transported by moving the shoulder and elbow through the activation of more proximal muscles which do not receive direct input from corticospinal neurons. It has been shown that specific brain lesions can alter one component without affecting the other (Brinkman & Kuypers, 1972; Haaxma & Kuypers, 1975; Kuypers, 1973). For example, damage to the pyramidal tract (which contains corticospinal projections) impairs fine finger control, including the grasping of objects. In contrast, damage to the extra-pyramidal tract (which motor pathways lie outside the corticospinal tract) impairs gross arm movements such as bringing the hand towards an object. In addition, the maturation of these neural pathways follows a different time course. The pyramidal tract matures after the extra-pyramidal tract which might explain why fine finger control is only achieved after gross movements can be controlled (Lawrence & Hopkins, 1972).

Jeannerod (1981, 1984) also provided behavioral evidence in support of his two component model of reaching and grasping. In these experiments, participants were asked to reach and grasp for objects whose intrinsic (i.e., size) and extrinsic properties (i.e., position) were manipulated. Wrist movements (transport component) featured the typical bell-shaped velocity profile also observed in aiming movements (Flash & Hogan, 1985).

Moreover, the separation between the thumb and the index finger (i.e., grip aperture, grasp component) first progressively increased before the grip was gradually closed again until the object is grasped. Jeannerod (1981) showed that changing the size of an object (intrinsic parameter) did not affect the transport component (i.e., wrist position and velocity profiles were similar regardless of object size), but affected the grasp component (i.e., maximum grip aperture scaled with object size). In contrast, changing the position of an object (extrinsic parameter) affected the transport component (i.e., peak velocity increased with target distance), whereas grip aperture profiles (grasp component) remained similar. Nevertheless, there appear to be strong temporal dependencies between these two components. For example, maximum grip aperture (MGA) depends on the speed of the wrist movement. When participants reach for objects more quickly, the distance between the thumb and index finger is larger when they reach for the same object more slowly (Wing, Turton, & Fraser, 1986). In addition, the point at which MGA occurs has been reliably reported to be between 60-70 % of the reach-to-grasp duration. This corresponds to the point in time when the hand begins the slow-approach phase of the movement (Castiello, 2005; Jeannerod, 1984). Despite the fact that subsequent studies have found that intrinsic and extrinsic object properties do not exhibit independent effects on either the grasp or the transport component, respectively (e.g., Chieffi & Gentilucci, 1993; Jakobson & Goodale, 1991; Smeets & Brenner, 1999), this ‘classic approach’ to grasping movements has substantially contributed to the current understanding of reaching and grasping.

1.5.3 Context effects

These studies certainly demonstrate that movement kinematics are highly influenced by the properties of an object. However, they do not address Napier’s claim that the intended activity should be reflected in movement selection. Although Napier’s claim concerned grasp selection, it might well be argued that if grasp selection is sensitive to future task demands, the kinematics should be as well. Initial evidence in support of this notion was provided by Marteniuk, MacKenzie, Jeannerod, Athenes, and Dugas (1987). They systematically varied the movement context in which reaching and grasping movements were performed to examine whether motor planning relies on relatively abstract and general internal representations (Keele, 1981; Schmidt, 1975) which can be scaled in the temporal and spatial domain, or whether motor planning is influenced by task specific constraints (i.e., context effects) which encode past experience and sensory consequences of an action. In one experiment, participants reached and grasped a disk to either throw it into a large container or place it into a tight fitting container. Although the initial part of the action sequence (i.e., reach toward and grasp the disk) was identical in both conditions, Marteniuk et al. (1987) observed longer movement times for grasping prior to fitting compared to grasping prior to throwing. More specifically, the lengthening of the movement time was primarily due to increases in the time taken to decelerate toward the target (i.e., the decelerative phase of the movement). The authors concluded that the intent of the actor influences motor planning processes, and speculated that the lengthening of the deceleration phase allows participants to use more sensory information in order to better cope with the increased precision demands when placing the disk into the tight container. In other words, action sequences are not produced by planning and then executing one step at a time. Rather, a plan is generated that already contains information about steps that occur later in a sequence.

The existence of plans that encode information of future task demands is not limited to manual tasks, but is well known in connection with speech co-articulation, for instance in a phenomenon called anticipatory lip rounding. Here, the way a sound is produced depends on what sounds will follow (Fowler, 2007). Using object manipulation tasks, several studies have further confirmed that reach-to-grasp kinematics are sensitive to the action goal of a task (e.g., Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Santello, Massaccesi, & Castiello, 2006; Armbrüster & Spijkers, 2006; Johnson-Frey,

McCarty, & Keen, 2004). Such context effects demonstrate that single movements are not planned in isolation, but as part of a larger action sequence. In other words, context effects suggest that motor planning and control involve internal representations of task demands that go beyond immediately available perceptual information, and are formed well in advance of the actions that actually being performed (Johnson-Frey et al., 2004).
In this context, the concept of different orders of motor planning was recently introduced by Rosenbaum and colleagues (Rosenbaum et al., 2013; Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012). Whereas first-order planning reflects adjustments to immediate available perceptual information or task demands such as adjusting the grip to the size of an object (e.g., Jeannerod, 1981, 1984), second-order planning involves adjustments not only to immediate task demands, but also to demands of the next task to be performed. Theoretically, this concept can be carried out ad infinitum, making it possible to examine third- or even higher-order motor planning. In this sense, second- and higher-order motor planning effects can be viewed as manual analogues of speech co-articulation effects (Rosenbaum et al., 2013).

1.6 Grasp posture planning

1.6.1 The end-state comfort effect

The influence of future task demands or intended action goals has also been studied by examining the grasp postures that people use to manipulate objects. The logic underlying this approach is analogous to that used in the kinematic studies of Marteniuk et al. (1987): If the same object is grasped differently depending on different goals or future task demands, then the participants' action plans must encode information about these task demands so as to adjust their initial grasp posture.
Much of the research carried out on grasp posture planning has focused on second-order

planning effects. The typical experimental paradigm required participants to reach and grasp an object with one subsequent object manipulation (e.g., place the object somewhere else). Initial studies on second-order grasp posture planning were conducted by Rosenbaum et al. (1990). In this now seminal paper, Rosenbaum et al. (1990) asked participants to grasp a horizontally arranged bar and place either its left or right end into a target disk located to the left or the right side of the bar's initial position. The authors found that, regardless of target location, participants switched their initial grasp posture depending on the required end orientation of the bar. Specifically, when the right end was to be brought to the target disk, participants would adopt an initial overhand grasp posture. Conversely, when the left end was to be brought to the target disk, participants would initially grasp the bar with an underhand grasp. Thus, participants always selected an initial grasp that afforded a thumb-up posture at the end of the movement. This final posture allowed the forearm to be near the middle of its range of motion. As psychophysical ratings confirmed, the terminal thumb-up was rated to be more comfortable compared to a thumb-down posture. In another experiment Rosenbaum, Vaughan, Barnes, and Stewart (1993), participants grasped a handle connected to a disk and rotated the handle to a designated target. Again, the way participants initially took hold of the handle depended on the final handle orientation such that they ended the handle-rotation in a comfortable posture. Since its original description (Rosenbaum et al., 1990), the end-state comfort effect has been reproduced in a variety of different experiments employing second-order planning tasks (e.g., Cohen & Rosenbaum, 2004; Herbort & Butz, 2010, 2011, 2012; Hughes, Seegelke, & Schack, 2012; Hughes, Seegelke, Spiegel, et al., 2012; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992; Rosenbaum et al., 1993; Seegelke et al., 2011; Short & Cauraugh, 1997, 1999).

For example, employing a slightly modified version of the bar-transport task, Hughes, Seegelke, Spiegel, et al. (2012) demonstrated that even when faced with an unexpected change in action goal (i.e., the initial stimulus indicated that the left end of the bar is to be brought to the target but as soon as the movement was initiated a secondary stimulus indicated that the right end is to be brought to the target), participants will make corrections to their initial grasp posture plan to ensure comfortable end-postures. Thus, planning for comfort at later stages appears to be a dominant action selection constraint during unimanual object manipulation tasks. More generally, this phenomenon is a nice example of goal-directed motor planning, and has been taken to support the idea that participants represent future body postures and select initial grasps in anticipation of these forthcoming postures. In support of this view, Hughes, Seegelke, Spiegel, et al. (2012) reported that the formation of end-state compliant grasp postures started immediately after reach-to-grasp onset, suggesting that the selection of appropriate grasp posture takes place very early, even before movement onset (see also Chang, Klatzky, & Pollard, 2010; Herbort & Butz, 2010; Johnson, 2000; Lippa & Adam, 2001; Rosenbaum et al., 1992; Zimmermann, Meulenbroek, & Lange, 2011 for similar conclusions). Together, these findings are not only congruent with early models of motor control (e.g., Bernstein, 1947; Lashley, 1951; Woodworth, 1899), but also fit nicely with current conceptions of the planning and control of goal-directed actions (e.g., Hommel et al., 2001; Knuf et al., 2001; Rosenbaum et al., 2001; Schack, 2004) which highlight the role of perceptual effect representations (e.g., visual, proprioceptive, auditory) in the planning and control of voluntary actions.

1.6.2 Explanations for the end-state comfort effect

Several explanations for the end-state comfort effect have been put forward such at the working backward hypothesis (Rosenbaum et al., 1990), the fatigue hypothesis (Rosenbaum et al., 1990), minimizing time in awkward postures (Rosenbaum et al., 1990; Seegelke et al., 2011), exploiting elastic energy (Rosenbaum & Jorgensen, 1992; Rosenbaum et al., 1990), gravity (Rosenbaum, van Heugten, & Caldwell, 1996), or the precision hypothesis (Hughes, Seegelke, & Schack, 2012; Rosenbaum et al., 1996, 1993; Short & Cauraugh, 1999). Whereas most of these hypotheses were discarded early on, the precision hypothesis has attracted significantly more attention. The precision hypothesis states that the likelihood of planning for comfortable postures at the end of the movement is related to the precision demands necessary for task completion (Rosenbaum et al., 1993). As movements can be corrected more rapidly when the limbs are near the middle of their range of motion (Rosenbaum et al., 1996), comfortable postures allow for more precise movement control. Because the tasks employed typically required more precision at the end of the movement than at the start, it is likely that end-state comfort per se was not the driving factor. Initial evidence in favor of the precision hypothesis was provided by Rosenbaum et al. (1996). They employed the same paradigm as in Rosenbaum et al. (1993) with the exception that when the handle was rotated to the designated target a bolt would drop into a hole at this location. This manipulation would allow participants to just broadly rotate the handle towards the target position without the need to precisely position the handle at the end of the movement. Congruent with the precision hypothesis, the authors found a reduced tendency for end-state comfort (i.e., half of the participants no longer adjusted their initial grasp posture to the required target position but instead tolerated awkward final postures in some conditions. Further evidence supporting the precision hypothesis comes from a study by Short and Cauraugh (1999). Participants picked up a dowel and touched either end to a large or small target on a wall. The authors observed that participants were more likely to satisfy end-state comfort for the small as compared to the large targets. In addition, error analysis revealed that participants showed greater accuracy in object placement when in a comfortable posture. Together these findings were interpreted as evidence that control, rather than comfort, was likely to be the major determinant in participants' grasp choices.

This idea was further confirmed by subsequent studies performed by Rosenbaum and colleagues (Cohen & Rosenbaum, 2004; Rosenbaum, Halloran, & Cohen, 2006) in which participants could select a grasp posture from a continuum of possible solutions. Cohen and Rosenbaum (2004) asked participants to grasp a plunger to transport it from a home position (located at a fixed height) to one of five target positions located at different heights. Congruent with previous findings, they observed that the higher the target position the lower participants initially grasped the plunger (and vice versa), indicating that participants planned their actions such their limbs would be in comfortable position when placing the plunger to the target. In a later experiment, Rosenbaum et al. (2006) examined whether this grasp height effect would be modulated by concern for control rather than comfort. To this end, they manipulated the precision demands by adding rings of small or large diameter at both the home and the target platform. The authors reasoned that if participants planned for control rather comfort, the grasp height effect should be attenuated (i.e., participants should grasp the plunger lower if precision demands were high). The results confirmed this prediction, lending further support to the claim that control rather than comfort is likely to be the relevant constraint on action selection (see also Künzell et al., 2013).

1.6.3 Retrospective effects

The tendency to select initial grasp postures that afford easy-to-control final postures indicates that future task demands influence current action selection (i.e., prospective planning). However, there is also evidence that grasp posture planning is subject to retrospective effects. That is to say, current grasp selection is not only influenced by upcoming grasp postures but also by recently performed movements. Such hysteresis or sequential effects in the context of object manipulation were first described by Rosenbaum and Jorgensen (1992). In this task, participants grasped a dowel using an underhand or overhand grasp and placed either the left or the right end to one of 14 vertically arranged target positions. The critical finding of this study was that the point in which participants switched from an underhand to an overhand depended on the order (ascending vs. descending) in which the targets were successively touched. Participants persisted in using an underhand grasp longer when performing the task in an ascending order, whereas they persisted in using an overhand grasp longer when performing the task in a descending order. Thus, current grasp selection was influenced by the type of grasp used in the previous trial. The presence of sequential effects have been reported in subsequent studies (Cohen & Rosenbaum, 2004; Kent, Wilson, Plumb, Williams, & Mon-Williams, 2009; Rosenbaum et al., 2006; Schütz & Schack, 2013; Schütz, Weigelt, Oderken, Klein-Soetebier, & Schack, 2011; Weigelt, Cohen, & Rosenbaum, 2007; Weigelt, Rosenbaum, Huelshorst, & Schack, 2009). For example, in the task of Cohen and Rosenbaum (2004), when participants returned the plunger from the target platform to the home platform, they grasped the plunger close to where they had grasped it before. The authors argued that if participants would have generated a new action plan for the return moves, the plunger should have been grasped at a similar height regardless of target height (as the home platform was located at a fixed height). However, given that grasp heights of the return moves were similar to that of the first moves, Cohen and Rosenbaum (2004) postulated that participants created a new action plan for the first move and then recalled and slightly modified this plan for the return moves. As the generation of a new action plan is associated with cognitive costs, relying on memory-based recall processes is an effective strategy to economize these costs.

However, similar mechanisms might also be involved in prospective action control. In a study by Studenka, Seegelke, Schütz, and Schack (2012), participants opened a drawer either without any subsequent action or with a subsequent object lift. When an object had to be grasped from the drawer, joint angles when opening the drawer were more similar to those that would be adopted when grasping the object. This outcome not only demonstrates that features of upcoming postures are reflected in preceding postures, but reflects the tendency of the central nervous system to minimize differences between immediately forthcoming and subsequent postures. More generally, this finding is consistent with the view that actions may be selected in a way that minimizes transitions through task space (Fowler, 2007; Jordan & Rosenbaum, 1989; Rosenbaum et al., 2013).

To sum up, there is a wealth of research that has examined action selection constraints in the context of object manipulation tasks requiring second-order planning. Action selection constraints have been studied in isolation, but there are several attempts that have contrasted these constraints in order to determine their relative importance in the constraint hierarchy. Among others, the end-state comfort effect has been contrasted with sequential effects (e.g., Cohen & Rosenbaum, 2004, 2011; Rosenbaum & Jorgensen, 1992), with the tendency to manipulate objects with the dominant hand (Coelho, Studenka, & Rosenbaum, in press), and the tendency for the hands to stay spatially coupled during bimanual actions (e.g., Fischman, Stodden, & Lehmann, 2003; Hughes & Franz, 2008; Hughes, Haddad, et al., 2011; Hughes, Reißig, & Seegelke, 2011; Hughes, Seegelke, & Reißig, 2014; Hughes, Seegelke, Reißig, & Schütz, 2012; van der Wel & Rosenbaum, 2010; Weigelt, Kunde, & Prinz, 2006).

1.6.4 Multi-segment object manipulation tasks

Given the corpus of work investigating the constraints that guide grasp posture planning, it is surprisingly that little work has considered object manipulation tasks that go beyond two action steps (i.e., multi-segment tasks). The first foray into this work was conducted by Rosenbaum et al. (1990) who extended the bar-transport paradigm to a three-segment object manipulation task. In this task, participants grasped the bar from a start location, placed either the left or the right end of the bar at a first target position, and subsequently placed the same or the other end at a second target position. The question of primary interest was whether participants would plan their movements to afford comfortable postures at the first or the second target position. The data revealed that participants adopted postures that were comfortable at the first but not the second target position. Furthermore, examination of comfort ratings confirmed that grasp choice could not be explained by minimizing awkwardness at the initial or the second position, or by minimizing overall awkwardness. Rather, minimizing awkwardness at the first target position was the best predictor for the observed grasp choices. Hence, the data from this experiment yielded no evidence for grasp posture planning beyond the second order.

Initial evidence that grasp posture planning during object manipulation tasks extends to action sequences requiring multiple movements was provided by Haggard (1998). Participants grasped an octagonal object and placed it into two, three, or five predetermined target slots. Each action sequence contained a critical target whose position was varied so that it was the first or the last target in the sequence. Haggard found that initial grasp postures varied depending on the specific action sequence, up to three movements in advance. Moreover, adjustments in initial grasp postures were more prominent when the critical target was the first in the sequence compared to when it was the last. This latter finding was taken as evidence that participants can plan more thoroughly for targets that occur earlier in an action sequence, and is indicative of a cognitive constraint in action selection during multi-segment object manipulation tasks (i.e., a gradient of advance planning).

Expanding on these findings, Hesse and Deubel (2010) demonstrated that people are capable of planning multi-segment object manipulation tasks holistically in advance even when the task requires manipulating multiple objects. They had participants reach and grasp a cylinder, place it on a target circle, and subsequently grasp and displace a bar that was positioned in one of three different orientations. It was found that the orientation of the bar at the end of the action sequence influenced the grasp orientations of the preceding segments (i.e., when grasping and placing the cylinder), and that grasp orientations in these segments were systematically shifted towards the final grasp orientation (i.e., when grasping the bar). These results are reminiscent of the findings of Studenka et al. (2012) mentioned earlier, and may reflect the tendency of the central nervous system to plan multi-segment action sequences in way that postural transitions between immediately forthcoming and subsequent postures are minimized (see also Rosenbaum et al., 2013).

Interestingly, Hesse and Deubel (2010) showed that when the precision demands of placing the cylinder were substantially increased (instead of placing the cylinder on a target circle, participants had to place it on a pin located at the center of the target circle), grasp orientations in the early movement segments were no longer influenced by the bar orientation at the end of the sequence. The authors concluded that the increased precision demands of the task might have required more planning resources, and thus prevented participants from planning the entire sequence in advance. As such, participants were forced to plan the movement in a sequential fashion.

1.7 Purpose of the dissertation and research questions

Taken together, there is a wealth of research that have examined second-order grasp posture planning during object manipulations tasks (see Rosenbaum et al., 2013, 2012, for reviews). In contrast there is clearly a dearth of studies that have looked at higher-order motor planning in the context of object manipulation (i.e., multi-segment object manipulation tasks). The lack of research in this area is indeed surprising, given that movements in everyday tasks do not occur in isolation, but are often embedded within a larger action sequence. Consider, for example, the task of making a cup of tea. To achieve the task goal, one has to grab a cup from the cupboard, place it on a table, put a tea bag into the cup, and pour water into it. Without even considering subsequent tasks such as stirring or drinking, it becomes apparent that such a task necessitates the appropriate sequencing of multiple action steps in order to successfully achieve the task goal. How our central nervous system accomplishes this is still not well understood. Consequently, the purpose of the present dissertation is to shed some light on these issues and examine action selection constraints during multi-segment object manipulation grasp posture planning. Specifically, it is of interest to investigate what action selection constraints influence or determine multi-segment grasp posture planning, how multiple constraints might interact with one another, and how their relative importance might change depending on several factors. The current dissertation focuses on the following action selection constraints and their interdependencies during multi-segment object manipulation tasks – (1) the tendency to select grasp postures that allow for control at later stages (end-state comfort effect), (2) the tendency to minimize postural transitions between immediately forthcoming and subsequent postures, and (3) a cognitive planning gradient, which indicates that action segments which occur earlier in a sequence are considered stronger in an action plan.

1.7.1 Interaction between biomechanical and cognitive factors

The tendency to select grasp postures that allow for control at later stages (end-state comfort) has been extensively studied during second-order object manipulation tasks (Rosenbaum et al., 2013, 2012), and has been found to be a quite robust selection constraint during unimanual actions. In contrast, the only study that explicitly addressed end-state comfort during a three-segment object manipulation task failed to demonstrate end-state comfort, but instead found intermediate-state comfort (i.e., minimizing awkwardness after the first, but not the second object transport, Rosenbaum et al., 1990). Although this can certainly indicate that people did not plan beyond the first object placement in this task, it seems unlikely given that subsequent studies showed that people are capable of planning further ahead. However, it is possible that the first target position was considered to a stronger degree due to a planning gradient (Haggard, 1998). Third, intermediate comfort may be generally favored over end-state comfort, but previous studies could not distinguish between intermediate- and end-state comfort as the first position was always the last target position. The aforementioned reasons point to a potential drawback of the initial end-state comfort effect studies. Specifically, the majority of studies employed a two-alternative forced choice procedure. That is to say, these tasks were restricted to a binary grasp choice in which participants could select either an overhand or and underhand grasp. Consequently, in the critical conditions participants could achieve comfort at only one position, but were unable to distribute comfort among two or more locations. More recently, researchers have begun to employ tasks and techniques in which participants can select from a continuous range of possible grasp postures, hence allowing for a more subtle examination of action selection constraints (e.g., Herbort & Butz, 2010, 2012; Schütz et al., 2011; Zhang & Rosenbaum, 2008). In general, these studies have indicated that the sensitivity toward comfortable end-states is not as pronounced as previously assumed. For example, in Herbort and Butz (2010) participants grasped a circular knob and rotated it 45°, 90°, or 135° in a clockwise or counterclockwise direction. Although participants selected initial grasp postures that were generally compatible with end-state comfort, the extent of the sensitivity toward comfortable final postures was influenced by the direction and the degree of rotation, suggesting that participants did not strictly optimize end-state comfort. Rather, these findings indicate that participants plan their movements in way that allow for comfortable or controllable postures at multiple locations.

The aim of Chapter 2 is to examine grasp posture planning during a three-segment object manipulation task in which participants can select their grasp postures from a continuum of possible solutions. Specifically, it is of interest to examine the extent to which participants will adjust their initial grasp postures to the first and the second target position. In addition, such a task affords the examination of the interaction between biomechanical constraints (i.e., planning for comfort) and cognitive constraints (i.e., a planning gradient), as well as the relative weighting of these constraints within a task-specific constraint hierarchy. Moreover, the secondary aim of Chapter 2 is to examine if, and possibly to what extent, the relative weighting of biomechanical and cognitive constraints changes across several repetitions. To this end, participants performed a three-segment object manipulation task (as well as two- and one-segment tasks as control conditions) in which they grasped a cylindrical object from a home position, placed it at a first target position, and subsequently at a second target position. The position of the targets was manipulated such that the degree of required object rotation (ranging from 0° to 180°) between the home and the first target position, and between the first and the second target position, differed. It is proposed that the extent to which participants adjust their initial grasp postures to the first and second target position will provide insights into the influence of biomechanical and cognitive constraints on motor planning. In addition, adaptations in initial grasp posture adjustment over repetitions would provide evidence that the relative influence of these constraints is not fixed, but can change with experience.

1.7.2 Comfort planning vs. postural transition minimization

Besides selecting initial grasp postures that allow for control at later stages in the movement sequence, it has been proposed that actions may be selected in a way that minimizes postural transitions between immediately forthcoming and subsequent postures (Rosenbaum et al., 2013; Studenka et al., 2012). Congruent with that idea, Hesse and Deubel (2010) found that during the planning of a multi-segment object manipulation task, grasp orientations at early movement segments were systematically steered towards grasp orientations at the end of the movement sequence. A notable difference between this and previous studies is that the first placement of the object did not require any specific orientation (i.e., the first target position was unconstrained). In addition, in this study participants manipulated the objects using a precision grip (i.e., grasping with the thumb and index finger only). Functional (e.g. Napier, 1956), behavioral (e.g., Castiello, Bennett, &

Paulignan, 1992; Gentilucci et al., 1991), as well as neurophysiological differences (e.g., Ehrsson et al., 2000; Westerholz, Schack, & Koester, 2013) between power and precision grasps have been appreciated before (see Castiello & Begliomini, 2008, for a review), making it reasonable to assume that the cognitive mechanisms underlying either type are quite different as well. In other words, action selection constraints might we weighted differently depending on the type of grip employed.

Consequently, the aim of Chapter 3 is to examine the interplay between the tendency to select grasp postures that allow for comfortable or easy-to-control postures at later stages and the tendency to minimize differences between immediately forthcoming and subsequent postures during a three-segment object manipulation task in which a power grasp is employed. To this end, we adapted the experimental task described in Chapter 2 such that the object orientation at the first (intermediate) target position was unconstrained, and participants were free to place the object in any desired orientation (similar as in Hesse & Deubel, 2010). Thus, participants reached and grasped a cylindrical object from a home position, placed it at an intermediate target position in a freely chosen orientation, and subsequently placed it at one of four final target positions in a predetermined orientation. If planning comfort at later stages is the predominant action selection constraint, it is expected that an inverse relationship between initial grasp postures adjustment and final target position will be observed (similar as in Zhang & Rosenbaum, 2008). In addition, given that object orientation at the intermediate target position was unconstrained, participants would additionally have the possibility to satisfy intermediate-state comfort, which should be expressed in invariant intermediate grasp postures. In contrast, if postural transitions are minimized, initial grasp postures should not be adjusted to final target orientation. Furthermore, if transitions between initial and intermediate postures are minimized, these postures should be similar. In contrast, if transitions between intermediate and final postures are minimized, those postures should be similar.

1.7.3 Extension to two-object manipulation tasks

The study of Hesse and Deubel (2010) also demonstrated that advance planning is not limited to tasks involving a single object. Rather, their data indicated that participants are capable of planning the entire action sequence holistically in advance even if multiple objects are manipulated. Chapter 4 expands on this work and aims to investigate whether people plan for comfort at later stages during a multi-segment object manipulation task in which two objects are manipulated. To address this question, participants opened a drawer, grasped an object from inside the drawer, and subsequently placed the object on a table in one of three different target orientations. If participants plan the entire sequence in advance, initial grasp postures (i.e., when opening the drawer) and intermediate grasp postures (i.e., when grasping the object) should be influenced by the final target orientation. However, given that participants did not have to maintain their initially selected grasp throughout the entire sequence, it is also possible that only intermediate grasp postures are influenced by the final target orientation. Moreover, if participants plan for end-state comfort, intermediate but not final grasp postures should be influenced by the final target orientation.

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2 Grasp posture planning during multi-segment object manipulation tasks – interaction between cognitive and biomechanical factors

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2.1 Abstract

The present study examined adaptations in the planning of initial grasp postures during a multi-segment object manipulation task. Participants performed a grasping and placing task that consisted of one, two, or three movement segments. The position of the targets was manipulated such that the degree of object rotation between the home and temporally proximal position, and between the temporally proximal and distal target position, varied. Participants selected initial grasp postures based on specific requirements of the temporally proximal and temporally distal action segments, and adjustments in initial grasp posture depended on the temporal order of target location. In addition, during the initial stages of the experimental session initial grasp postures were influenced to a larger extent by the demands of the temporally proximal segment. However, over time, participants overcame these cognitive limitations and adjusted their initial grasp postures more strongly to the requirements of the temporally distal segment. Taken together, these results indicate that grasp posture planning is influenced by cognitive and biomechanical factors, and that participants learn to anticipate the task demands of temporally distal task demands, which we hypothesize, reduces the burden on the central nervous system.

2.2 Introduction

Movements performed in daily life rarely occur in isolation, but are most often embedded within a task consisting of multiple actions. For example, when reaching for a coffee carafe the goal is not merely to grasp the handle of the carafe, but to do something with the carafe once it has been grasped. Although the "something" might differ depending on the situation, research has shown that action goals (e.g., pouring coffee from the carafe into a cup) exert considerable influence over the planning and execution of reach-to-grasp movements (e.g., Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Santello, Massaccesi, & Castiello, 2006; Armbrüster & Spijkers, 2006; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). For example, in Ansuini et al. (2008) participants reached for a bottle filled with water and then either 1) grasped the bottle without any subsequent action, 2) lifted and threw the bottle into a container, 3) lifted and placed the bottle on a target circle slightly larger than the bottle, 4) lifted and poured water from the bottle into a plastic container, or 5) lifted and passed the bottle to the experimenter. Although the initial part of the movement sequence (i.e., reach toward and grasp the bottle) was identical for all conditions, the authors observed that reach duration and the time course of hand shaping (measured at the level of individual finger joints) were influenced by the subsequent action.

The influence of action end-goal has also been shown to influence initial grasp posture planning during manual action sequences (e.g., Herbort & Butz, 2010, 2012; Hughes, Seegelke, & Schack, 2012; Hughes, Seegelke, Spiegel, et al., 2012; Rosenbaum et al., 1990; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992; Seegelke, Hughes, & Schack, 2011; Seegelke, Hughes, Schütz, & Schack, 2012; Zhang & Rosenbaum, 2008). In a study by Zhang and Rosenbaum (2008) participants placed their right hand on top of a round object and slid the object from the start position to one of five final target positions. Their results showed that initial hand orientation varied as a function of the final target position such that participants placed their hands on the object at an angle that was inversely related to the final angle of the hand. Complementing this, Herbort and Butz (2010) had participants grasp a circular knob and turn it 45°, 90°, or 135° in a clockwise or counterclockwise direction. In line with the results of Zhang and Rosenbaum (2008), the authors found that initial forearm angles were inversely related to the final target angles, and that knob rotation direction had a considerably stronger influence (compared to the extent of rotation).Their data also yielded insights about the temporal nature of grasp posture formation during object manipulation. Overall, forearm rotations were evident at 25 % of the reach-to-grasp phase, and reaction times were shorter when participants were given advance information about the required knob rotation, compared to when no advance information was available. Based on these results the authors argued that grasp postures are selected prior to movement onset, and are strongly influenced by the action goals of the task.

Haggard (1998) was one of the first to investigate planning of initial grasp postures during multi-segment action sequences (but see also Rosenbaum et al., 1990). In that study, participants grasped an octagonal object and subsequently placed it to two, three, or five different targets, depending on condition. Each movement sequence contained a critical target whose position was varied so it was either the first or the last target in the sequence. Haggard found that initial grasp choice differed depending on the specific movements they performed for sequences that consisted of up to three movements. Moreover, adjustments in initial grasp posture were more prominent when the critical target was the first in the sequence as compared to when it was the last. These results provide evidence that the central nervous system is able to integrate multi-segment movement sequences into a single action plan and that participants can better plan for steps that occur early in a movement sequence (i.e., a gradient of advance planning).

Although previous research has provided some insights into the planning of multi-segment actions (Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012), they have not assessed variations in grip choice across several repetitions. Accordingly, questions on the stability of initial grasp choice across several replications remain unanswered. Building on this work, the aim of the current study was to examine the influence of target orientation and sequence length on grasp posture planning during a multi-segment object manipulation task, and to ascertain whether initial grasp postures adapt to different task constraints (biomechanical and cognitive) over time. In this task, participants performed a grasping and placing task consisting of one, two, or three movement segments. In the one-segment movement sequence participants grasped a cylindrical object from a home position and lifted it upwards 10 cm. In the two-segment movement sequence, participants grasped a cylindrical object from a home position and placed it on a first (temporally proximal) target position. In the three-segment movement sequence participants grasped a cylindrical object from a home position, placed it on a first target position (temporally proximal), and without adjusting their grasp posture placed it on a second target position (temporally distal). We also manipulated the position of the targets such that the degree of object rotation (ranging from 0° to 180°) between the home and temporally proximal target position and between the temporally proximal target and temporally distal target position differed.

Based on research indicating that grasp postures are planned prior to movement initiation (e.g., Herbort & Butz, 2010; Hughes, Seegelke, Spiegel, et al., 2012; Rosenbaum et al., 1992), and that participants can plan up to three movements in advance (e.g., Haggard, 1998; Hesse & Deubel, 2010), we hypothesized that initial grasp choice would be influenced by the first (temporally proximal) and second temporally distal targets of the movement. Moreover, given the research demonstrating that holistic grasp planning decreases with the number of action segments (Haggard, 1998), we expected that the temporally proximal target would have a stronger influence on initial grasp postures than the temporally distal target. Further, if participants adapt their movement plans in response to the imposed biomechanical (i.e., target orientation) and cognitive (i.e., target order) task constraints, we expected to observe changes in initial grasp over repetitions. Such a finding would be consistent with the hypothesis that grasp posture planning relies on a flexible, rather than a static, constraint hierarchy (Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; van der Wel & Rosenbaum, 2010). Last, given the large corpus of research indicating a proportional relationship between the reaction time and the complexity of an action sequence (e.g., Christina, 1992; Fischman, 1984; Henry & Rogers, 1960; Klapp, 2010; Sternberg, Monsell, Knoll, & Wright, 1978), we hypothesized that movement initiation time (MIT) and approach time (AT) would increase as the number of steps and the required degree of object rotation in the action sequence increases.

2.3 Experiment 1

2.3.1 Methods

Participants 20 students from Bielefeld University (*M* age = 24.3 years, *SD* = 4.3, 16 women, 4 men) participated in this experiment. All participants were right-handed (*M* score = 96.7, *SD* = 14.9) as assessed using the Revised Edinburgh Handedness Inventory (Dragovich, 2004) and were paid 5 € for participation. Participants had normal or corrected to normal vision, and did not have any known neuromuscular disorders. The experiment was conducted in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

Apparatus and stimuli The experimental apparatus is shown in Figure 2.1AB. The set-up was positioned on a height adjustable shelf (200 cm $\times$ 60 cm). White paper circles (10.5 cm in diameter, with a 9 cm $\times$ 2cm protrusion) were taped flat to the surface of the shelf and served to indicate the home, center, and outer targets. The home and outer targets were arranged in a semi-circular fashion, each separated by 45°. Viewed from the participant's perspective, the home target was located at 0°, while the outer targets were located at -90°, -45°, 45°, and 90°, as indicated by the protrusions. The center target was located midway between the -90° and 90° outer targets. Protrusions radiated from the left (center target angle -90°) and the right (center target angle 90°) of the white circle and indicated the respective center target orientations. The manipulated object was a grey PVC cylinder (5 cm in height, 10 cm in diameter) that had a protrusion (8.5 cm $\times$ 1 cm) which extended from the bottom of the object (Figure 2.1C).

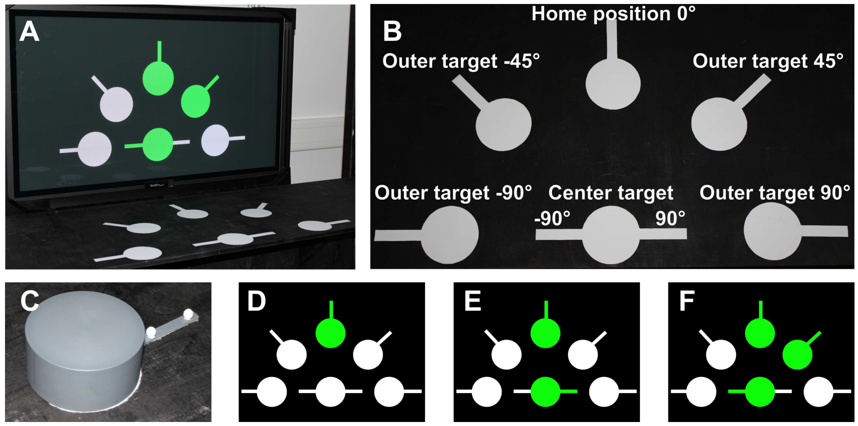

Figure 2.1: Experimental setup and stimuli. A Front view of the experimental setup. The stimulus depicts a three-segment movement sequence in which the object is to be grasped from the home position, placed to the -90° center target, and then to the 45° outer target. B Top view of the experimental setup. C Manipulated object. D-F Exemplary stimuli indicating the required center target and outer target object orientation for a D) one-segment sequence in which the object is to be grasped from the home position, lifted, and set down to the home position, E) two-segment sequence in which the object is to be grasped from the home position, placed to the 90° center target, and F) three-segment sequence in which the object is to be grasped from the home position, placed to the -90° center target, and then to the 45° outer target.

Visual stimuli were presented on a 127 cm flat screen monitor (Panasonic TH-50PF11EK) that was placed behind the shelf. The stimuli consisted of a visual representation of the set-up (bird's eye view) and displayed the required center target and outer target position (Figure 2.1DEF). Stimulus presentation was controlled via Presentation® (Neurobehavioral Systems).

Kinematic data was recorded using an optical motion capture system (VICON Motion Systems, Oxford, UK) consisting of 10 Bonita cameras with 200 Hz temporal and 1 mm spatial resolution. Three 14 mm diameter retro reflective markers were placed dorsally on the distal end of the third metacarpal (MCP), the styloid process of the ulna (WRP), and the styloid process of the radius (WRT) of the right hand. In addition, two 10 mm diameter markers were attached to the object protrusion (5 cm and 0.5 cm from the tip of the protrusion).

Procedure After filling out the informed consent form and handedness inventory, participant arm length and hip height were measured, and retro-reflective markers were placed on the right hand. The shelf was set to hip height and the home and target circles were arranged so that the distance from the center target to the home position and each outer target was 60 % of participant arm length. The participant stood in front of the shelf so that the right shoulder vertically coincided with the home and center target position.

At the start of each trial, an experimenter placed the object on the home position. The message ”Put your hand to the start position!” (in German) was displayed and the participant placed their hand on the shelf 10 cm to the right of the center target. A fixation cross was then presented for 500 ms, and after a random time interval (500 – 1500 ms), the stimulus was displayed and remained on the screen until the end of the trial. The participant then grasped the object from the home position and placed it to the required target(s), as indicated by the stimulus. At the end of the trial, the participant brought their hand back to the start position and waited for the next trial to begin. There were three different tasks. In the one-segment task, the participant grasped the object from the home position, lifted it and set it down to the home position (Figure 2.1D). The purpose of the one-segment task was to assess each participant's neutral initial hand angle. In the two-segment task, the participant grasped the object from the home position and placed it to the center target (-90° or 90°, Figure 2.1E). In the three-segment task, the participant grasped the object from the home position, then placed it to the center target (-90° or 90°), and subsequently to the outer target (-90°, -45°, 45°, or 90°, Figure 2.1F). Participants were told to grasp the object by placing their palm on top of the object and their fingers at the side, and not to change the selected grasp throughout the trial. Furthermore, the instructions emphasized that the task should be performed at a comfortable speed, and movement accuracy was stressed.

The one-segment task consisted of one condition and the two-segment task consisted of two conditions (center target -90° and 90°). For the three-segment task, there were 8 conditions comprised of the factors center target (-90°, 90°) and outer target (-90°, -45°, 45°, 90°). There were two blocks, within which each condition was repeated five times in a randomized order. This yielded a total of 110 trials. The entire testing session lasted approximately 45 minutes.

Data Analysis The 3D coordinates of the retro-reflective markers were reconstructed and labeled. Any missing data (less than 10 frames) were interpolated using a cubic spline and filtering using a Woltring filter (Woltring, 1986) with a predicted mean square error value of 5 mm^2 (Vicon Nexus 1.7). Kinematic variables were calculated using a custom written MatLab program (The MathWorks, Version R2010a). The wrist joint center (WJC) was calculated as the midpoint between WRT and WRP. In addition, two direction vectors were calculated, one pointing distally from the WJC to MCP (V1 = MCP-WJC), and a second one passing through the wrist (V2 = WRP- WRT). The hand center (HC) was defined on a plane normal to V1 $\times$ (V2 $\times$ V1), positioned palmar from MCP at a distance of (hand thickness + marker diameter)/2 in a way that (HC – WJC) and (HC – MCP) formed a right angle. The hand angle was calculated as the projection of the vector pointing distally from the WJC to the HC on the shelf plane (Figure 2.2). Thus, hand orientations with the fingers pointing up (12 o'clock position), left (9 o'clock position), right (3 o'clock position), and down (6 o'clock position) would result in hand angles of 0°, -90°, 90°, and 180°, respectively. Movement initiation time (MIT) was defined as the time period between stimulus onset to the time when the hand left the start position (movement onset). Approach time (AT) was defined as the time period between movement onset to the time the object was grasped (movement offset). Movement onset was determined as the time of the sample in which the resultant velocity of WJC exceeded 5 % of peak velocity. Movement offset was determined as the time of the sample in which the resultant velocity dropped below 5 % of peak velocity.

Trials performed in a non-instructed manner (moving prior to stimulus presentation, placing the object to a wrong target, changing the grasp during a trial) were counted as errors and were not included in analysis. Error trials comprised less than 6.8 % of the data, and were approximately equally distributed across condition and participants.

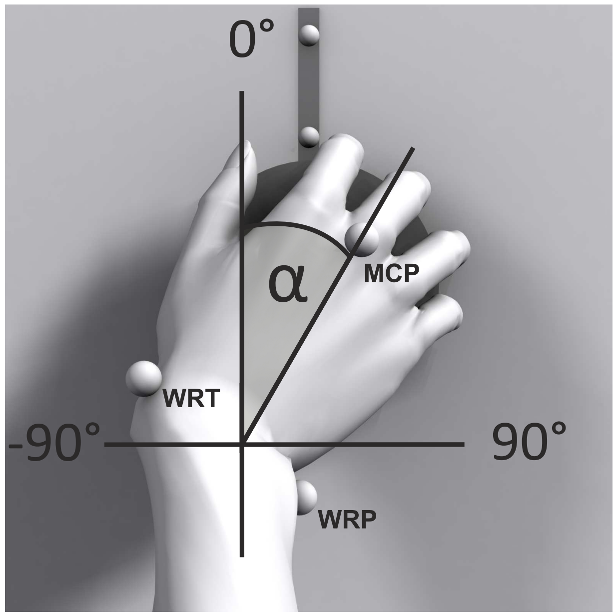

Figure 2.2: Calculation of hand orientation angle α.

2.3.2 Results

Movement initiation time MIT data are shown in Figure 2.3A and 2.3C. A block (block 1, block 2) $\times$ sequence length (one segment, two segment, three segment) repeated measures analysis of variance (RM ANOVA) revealed that average MIT's were shorter during the second block compared to the first block, $F(1,19) = 18.760$, $p < 0.001$, $\eta^2_p = 0.497$. MIT values increased with the number of segments in the action sequence, $F(2,38) = 9.287$, $p = 0.005$, $\eta^2_p = 0.328$. Post hoc tests (Bonferroni corrected) showed that MIT's were significantly longer for the three-segment sequence (806 $\pm$ 99ms),compared to both the one-segment (647 $\pm$ 67 ms, $p = 0.022$) and the two-segment sequence (669

$\pm$ 70 ms, p = 0.011). The difference between the one-segment and the two-segment sequence was not significant (p = 0.628, Figure 2.3A).

To investigate the influence of target orientation on MIT during the three-segment sequence condition, a block (block 1, block 2) $\times$ center target (-90°, 90°) $\times$ outer target (-90°, -45°, 45°, 90°)RM ANOVA was conducted. The main effect of center target [F(1,19) = 6.444, p = 0.020, $\eta^2{}_p$ = 0.253] and the interaction between center target and outer target was significant, F(3,57) = 5.366, p = 0.027, $\eta^2{}_p$ = 0.220. For sequences involving the -90° center target, MIT values were smallest for the -90° outer target, and increased for the -45°, 45°, and 90° outer target conditions. Post hoc tests (Bonferroni corrected) indicated that MIT values were smaller for the -90° outer target compared to the -45° and 45° outer target (p = 0.040 and 0.044, respectively). In contrast, for sequences involving the 90° center target the opposite pattern was found. Here, MIT values were smallest for the 90° outer target and increased for the 45°, -45°, and -90° outer target conditions. However, post hoc tests (Bonferroni corrected) did not reveal any significant differences (Figure 2.3C). In addition, there was a significant main effect of block, with shorter average MIT's during the second compared to the first block, F(1,19) = 9.690, p = 0.006, $\eta^2{}_p$ = 0.338.

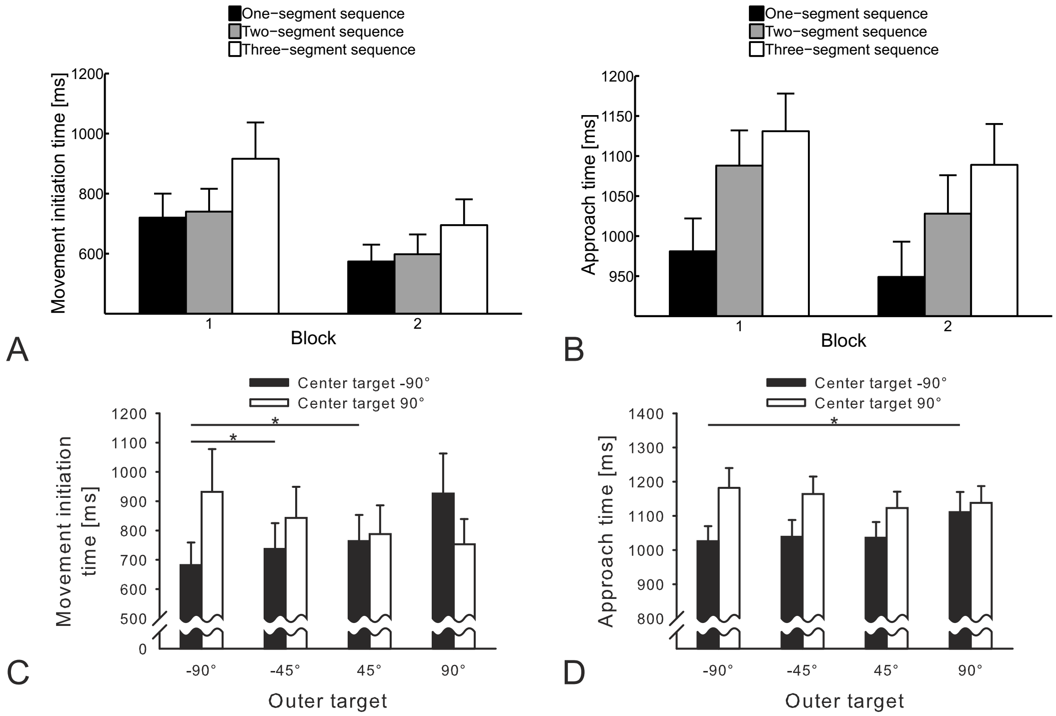

Figure 2.3: Average movement initiation times (MIT) and approach times (AT) as a function of sequence length and block in Experiment 1(panel A and B), as a function of center and outer target during the three-segment sequences in Experiment 1 (panel C and D), and as a function of center and outer target during the three-segment sequences in Experiment 2 (panel E and F). Error bars represent standard errors between subjects. Asterisks indicate significant differences (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$).

Approach time AT data are shown in Figure 2.3B and 2.3D. As with MIT, average AT values were smaller during the second compared to the first block, $F(1,19) = 5.700$, $p = 0.028$, $\eta^2{}_p = 0.231$. AT increased with the number of segments in the action sequence, $F(2,38) = 40.289$, p ¡ 0.001, $\eta^2{}_p = 0.680$. Post hoc tests (Bonferroni corrected) revealed that mean AT was longer for the three-segment action sequence (1110 $\pm$ 47 ms), compared to both the one-segment (965 $\pm$ 42 ms) and two-segment action sequence (1058 $\pm$ 44 ms), both *p's* < 0.01. Additionally, mean AT values were significantly longer for the two-segment, compared to the one-segment, action sequence ($p < 0.001$).

A block (block 1, block 2) $\times$ center target (-90°, 90°) $\times$ outer target (-90°, -45°, 45°, 90°) RM ANOVA conducted for the three-segment movement sequence revealed a significant main effect of center target [$F(1,19) = 42.175$, $p < 0.001$, $\eta^2_p = 0.689$], outer target [$F(3,57) = 4.145$, $p = 0.010$, $\eta^2_p = 0.179$], and a significant interaction between center target and outer target, $F(3,57) = 5.183$, $p = 0.013$, $\eta^2_p = 0.214$. For sequences containing the -90° center target, AT values were higher for the 90° outer target, compared to the -90°, -45°, and 45° outer target conditions. Post hoc tests (Bonferroni corrected) indicated significant differences between the -90° and the 90° outer target ($p = 0.017$). In contrast, for sequences containing the 90° center target, AT values were higher for the -90° outer target condition compared to the -45°, 45°, and 90° outer target conditions. However, post hoc analysis (Bonferroni corrected) did not reveal any significant differences (Figure 2.3D). Thus, similar to the MIT data, three-segment movement sequences AT values were higher for conditions that required a larger degree of object rotation between the center and outer targets.

In summary, the MIT and AT data indicate that participants planned the entire action sequence in advance and that the time to plan an action sequence depends on the number of steps in that sequence and the required degree of object rotation between the center and outer targets.

Grasp posture To analyze the influence of the center target on initial hand angles during the two-segment sequences, we conducted a block (block 1, block 2) × sequence (one-segment, two segment -90° center target, two-segment 90° center target) RM ANOVA. Mean hand angle during the one-segment movement sequence was -1.1 (± 1.9). During the two-segment movement sequences, initial hand angles were influenced by the center target [center target -90° = 13.7 ± 2.5°; center target 90° = -36.2 ± 3.2°, $F(2,38) = 114.738$, $p < 0.001$, $\eta^2_p = 0.858$]. The interaction between block and sequence was significant, $F(2,38) = 8.177$, $p = 0.007$, $\eta^2_p = 0.301$. For the one-segment trials and trials involving the -90° center target, mean initial hand angles increased from block 1 to block 2 ($p = 0.010$ and $p < 0.001$, respectively). In contrast, initial hand angles were similar in block 1 compared to block 2 for trials with the 90° center target (p = 0.113).

To examine the influence of center and outer target on initial grasp postures during the three-segment movement sequences (see Figure 2.4), we performed a block (block 1, block 2) $\times$ center target (-90°, 90°) $\times$ outer target (-90°, -45°, 45°, 90°) RM ANOVA. On average, initial hand angles were inversely related to both the center and outer target [main effect of center target: $F(1,19) = 149.204$, $p < 0.001$, $\eta^2_p = 0.887$; main effect of outer target: $F(3,57) = 7.484$, $p = 0.005$, $\eta^2_p = 0.283$]. However, these effects were modulated by a significant center target $\times$ outer target interaction, $F(3,57) = 3.575$, $p = 0.038$, $\eta^2_p = 0.158$. For sequences containing the -90° center target, post hoc tests (Bonferroni corrected) indicated significant differences between the -90° outer target and the -45° and 45° outer target (p = 0.028 and p = 0.031, respectively). For sequences containing the 90° center target, post hoc tests (Bonferroni corrected) revealed significant differences between the 90° outer target and the -45° and 45° outer target (p = 0.023 and p = 0.004, respectively).

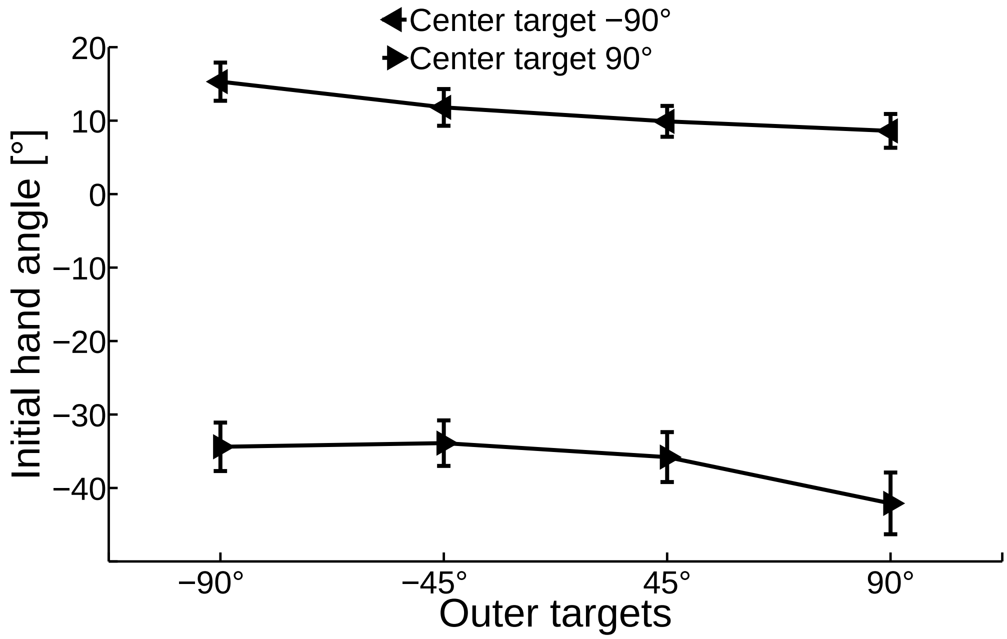

Figure 2.4: Initial hand orientation angles as a function of center and outer target for the three-segment sequences for Experiment 1. The -90° center target is represented by leftward facing triangles, while the 90° center target is represented by rightward facing triangles. Error bars represent standard errors between subjects.

To examine the magnitude of influence that the center and outer targets exerted on initial grasp postures across the experimental session, we conducted linear multiple regressions for the initial hand angles on the center and outer target separately for each block and participant. The slopes of these regressions provide an estimate of the contribution of the center and the outer target position on initial hand angles and are shown in Figure 2.5. A block (block 1, block 2) $\times$ target (center target, outer target) RM ANOVA indicated that the slopes for the best-fitting straight lines were significantly steeper for the center target (mean slope = -0.266), compared to the outer target (mean slope = -0.036), $F(1,19) = 150.421$, $p < 0.001$, $\eta^2_p = 0.888$. In contrast, slopes were similar during the second block (mean slope = -0.162) compared to the first block (mean slope = -0.140), $F(1,19) = 3.874$, $p = 0.064$, $\eta^2_p = 0.169$. These results indicate that the center target had a stronger influence on initial grasp postures than the outer target, but there was no evidence that the influence of the center and the outer target increased over the experimental session.

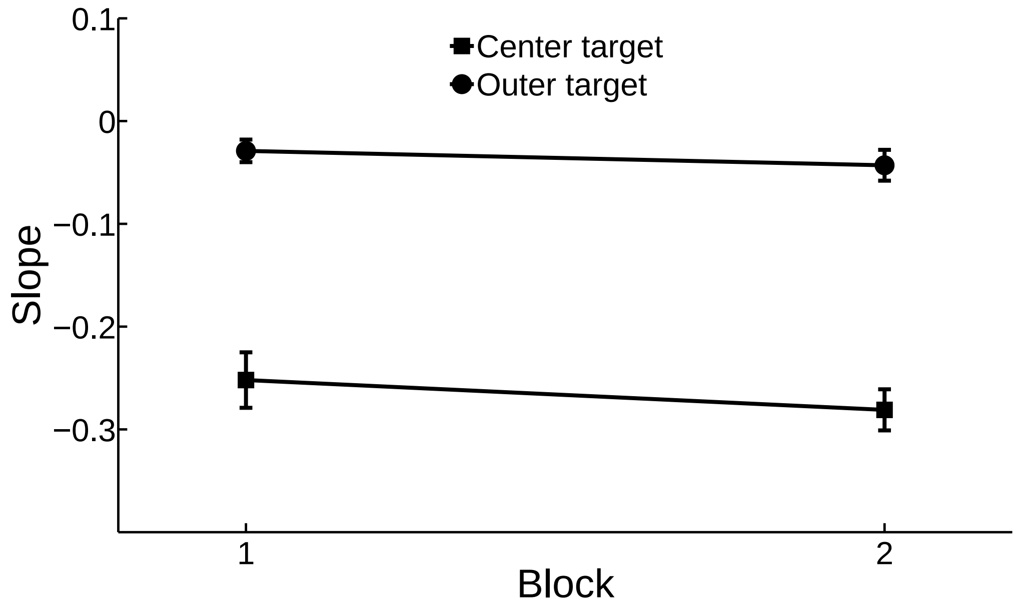

Figure 2.5: Slope values of the best-fitting straight lines for the center target (squares) and outer target (circles) as a function of block in Experiment 1. Error bars represent standard errors between subjects.

2.3.3 Discussion

In line with previous work (e.g., Fischman, 1984; Klapp, 1995, 2010; Sternberg et al., 1978), the results of Experiment 1 demonstrate that the time to plan a manual action sequence increased with the number of segments in the movement. MIT and AT values were significantly larger during the three-segment movement sequences compared to the one-segment and two-segment sequences. Moreover, MIT, AT, and initial grasp postures were influenced by both the center and the outer targets during the three-segment movement sequences. Specifically, MIT and AT increased with the required degree of object rotation between the first and second target, and initial grasp posture orientation angles were inversely related to hand orientation angle at the center and outer targets. These observations are consistent with Rosenbaum and colleagues (Rosenbaum et al., 1990; Zhang & Rosenbaum, 2008), who showed that participants select initial grasp postures that allow the limbs to be at, or close to, midrange positions (rather than at extreme positions) at the end of the movement. According to Rosenbaum, van Heugten, and Caldwell (1996), end postures that afford midrange limb positions ensure more control during object manipulation. Accordingly, the results of the present study suggest that participants selected initial grasp postures that allowed them to optimize control not only at the temporally proximal (i.e., center target), but also at the temporally distal target (i.e., outer target) in an action sequence. Together, these data demonstrate that manual action sequences are planned holistically in advance, that each segment was considered when planning their initial grasp postures, and that task demands that occur earlier in a sequence exhibit a stronger influence on initial grasp postures (i.e., a planning gradient, e.g., Haggard, 1998). Evidence that grasp planning improved across the experimental session was manifest only in the timing variables. In general, MIT and AT values decreased from block 1 to block 2, indicating that less time was required to plan the movement. In contrast, there was no evidence for adaptations in initial grasp posture across the experimental session.

However, the center and outer targets differed in spatial position, which may have placed unequal biomechanical constraints on arm configuration. As such, it is possible that the unequal biomechanical constraints between the center and outer target positions may have influenced initial grasp posture planning. Given that the results of Experiment 1 may have arisen because of biomechanical factors associated with spatial features of target positions or by cognitive limitations in advance planning we conducted a second experiment to dissociate between these two possibilities.

2.4 Experiment 2

In Experiment 2 we investigated whether the results from Experiment 1 arose from cognitive limitations in planning multi-segment actions or biomechanical factors related to the position of the targets. To distinguish between these two possibilities, we reversed the temporal order of the center and outer targets during the three-segment movement sequence. If the results of Experiment 1 are due to biomechanical factors, then we would expect to obtain results similar to Experiment 1. That is, the center targets would have a stronger influence on initial grasp postures than the outer targets. However, if the results of Experiment 1 are due to cognitive factors (i.e., the planning gradient hypothesis), we would expect that outer targets would have a strong influence on initial grasp postures, and that center targets would have a weaker effect on initial grasp postures. Last, these two hypotheses are not mutually exclusive, and as such there exists the possibility is that both cognitive and biomechanical factors contributed to the results of Experiment 1.

2.4.1 Methods

Participants 22 students from Bielefeld University (*M* age = 25.2 years, *SD* = 4.5, 16 women, 6 men) participated in this experiment. None of the participants participated in Experiment 1. All participants were right-handed (*M* score = 99.1, *SD* = 4.3) as assessed using the Revised Edinburgh Handedness Inventory (Dragovich, 2004) and were paid 5 € for participation. Participants had normal or corrected to normal vision, and did not have any known neuromuscular disorders. The experiment was conducted in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

Apparatus, procedure, and data analysis The apparatus and the stimuli were nearly identical to that used in Experiment 1. The only difference was that participants performed only the three-segment sequences, and the order of events was reversed such that participants grasped the object from the home position, placed it to an outer target (-90°, -45°, 45° or 90°), and subsequently to a center target (-90° or 90°).

The experiment consisted of 8 conditions, comprised of the factors center target (-90°, 90°) and outer target (-90°, -45°, 45°, 90°). There were two blocks, within which each condition was repeated five times in a randomized order. This yielded a total of 80 trials.

The entire testing session lasted approximately 30 minutes.

Trials performed in a non-instructed manner (moving prior to stimulus presentation, placing the object to a wrong target, changing the grasp during a trial) were counted as errors and were not included in analysis. Error trials comprised less than 2 % of the data, and were approximately equally distributed across condition and participants. The data were analyzed using RM ANOVAs with the factors block (block 1, block 2), center target (-90°, 90°), and outer target (-90°, -45°, 45°, 90°).

2.4.2 Results

Movement initiation time MIT data are shown in Figure 2.6A. There was a significant main effect of outer target [$F(3,63) = 7.531$, $p < 0.001$, $\eta^2{}_p = 0.264$] and a center target × outer target interaction, $F(3,63) = 10.099$, $p = 0.002$, $\eta^2{}_p = 0.325$. For sequences involving the -90° center target, MIT values were smallest for the -90° outer target, and increased for the -45°, 45°, and 90° outer target conditions. Post hoc test (Bonferroni corrected) indicated that MIT values were significantly larger for the 90° outer target compared to all other outer targets (all $p < 0.01$). In contrast, for sequences involving the 90° center target, MIT values were smallest for the 90° outer target and increased for the 45°, -45°, and -90° outer target conditions. Post hoc tests (Bonferroni corrected) revealed that MIT values were significantly larger for the -90° outer target compared to all other outer targets (all p's < 0.05).

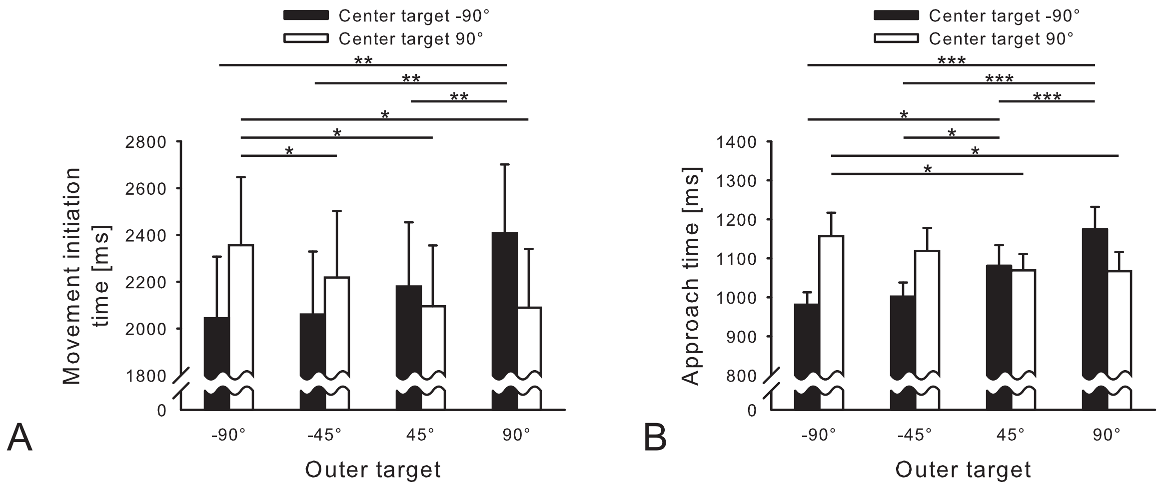

Figure 2.6: Average movement initiation times (MIT) and approach times (AT) as a function of center and outer target during the three-segment sequences in Experiment 2. Error bars represent standard errors between subjects. Asterisks indicate significant differences (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$).

Approach time AT data are shown in Figure 2.6B. The main effect of center target [$F(1,21) = 10.211$, $p = 0.004$, $\eta^2_p = 0.327$], the main effect of outer target [$F(3,63) = 5.908$, $p = 0.001$, $\eta^2_p = 0.219$] and the center target $\times$ outer target interaction was significant, $F(3,63) = 19.007$, $p < 0.001$, $\eta^2_p = 0.475$. AT values were smallest for the -90° outer target, and increased for the -45°, 45°, and 90° outer target conditions for sequences containing the -90° center target. Post hoc test (Bonferroni corrected) indicated that all comparisons were significant (all *p's* < 0.05), with the exception of the comparison between -90° and -45° outer targets. In contrast, AT values for sequences containing the 90° center target were smallest for the 90° outer target and increased for the outer target 45°, -45°, and -90°. Post hoc analysis (Bonferroni corrected) revealed that MIT values were significantly larger for the -90° outer target compared to the 45° and 90° outer targets ($p = 0.042$ and $p = 0.017$).

Grasp posture Initial hand postures were, on average, inversely related to both the center and the outer target [main effect of center target: $F(1,21) = 31.938$, $p < 0.001$, $\eta^2_p = 0.603$; main effect of outer target: $F(3,63) = 44.810$, $p < 0.001$, $\eta^2_p = 0.681$]. These effects were modulated by the center target × outer target interaction [$F(3,63) = 7.848$, $p = 0.001$, $\eta^2_p = 0.272$], such that the difference in initial hand angle between the -90° and 90° center target was more pronounced for the -90° and -45° outer targets, compared to the 45° and 90° outer targets (see Figure 2.7). For sequences containing the -90° center target, post hoc test (Bonferroni corrected) indicated significant differences between all outer targets (all p's < 0.05). For sequences containing the 90° center target, all comparisons except between the -90° and -45° outer target were significant (all p's < 0.05).

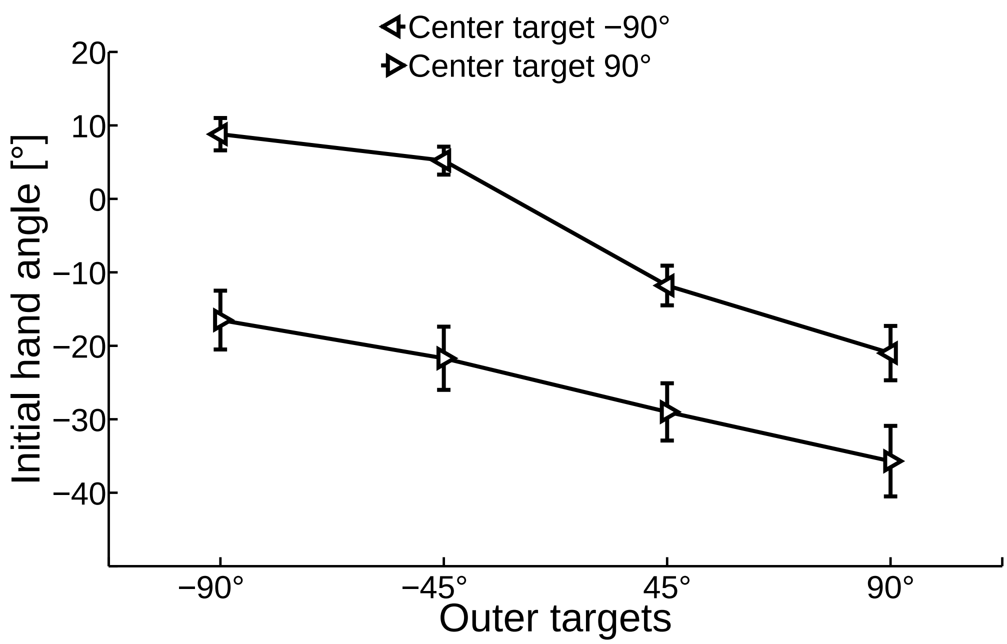

Figure 2.7: Initial hand orientation angles as a function of center and outer target for the three-segment sequences for Experiment 2. The -90° center target is represented by leftward facing triangles, while the 90° center target is represented by rightward facing triangles. Error bars represent standard errors between subjects.

Again, we conducted a block (block 1, block 2) × target (center target, outer target) RM ANOVA on the slopes. The negative correlation between initial hand orientation angle and center target and between initial hand orientation angle and outer target, respectively, was significant in each block (all p's < 0.01). The block × target interaction was significant, $F(1,21) = 4.891$, $p = 0.038$, $\eta^2_p = 0.189$. Slopes were initially (block 1) steeper for the outer target (mean slope = -0.156), compared to the center target (mean slope = -0.098, p = 0.043). However, this difference was abolished in block 2 as slope steepness decreased from block 1 to block 2 for the outer target (mean slope = -0.116), while it increased for the center target (mean slope = -0.135, p = 0.496). A Bonferroni corrected post hoc test on the difference scores (block 2 – block 1) revealed that the steepness of the slopes decreased for the outer target (mean slope difference = 0.040) while it increased for the center target (mean slope difference = -0.037), p = 0.038 (see Figure 2.8). This finding indicates that grasp postures were influenced by the outer target, more than the center target, during the initial phase of the experimental session. However, as the experimental session progressed, the influence of the center target increased, while the influence of the outer target decreased.

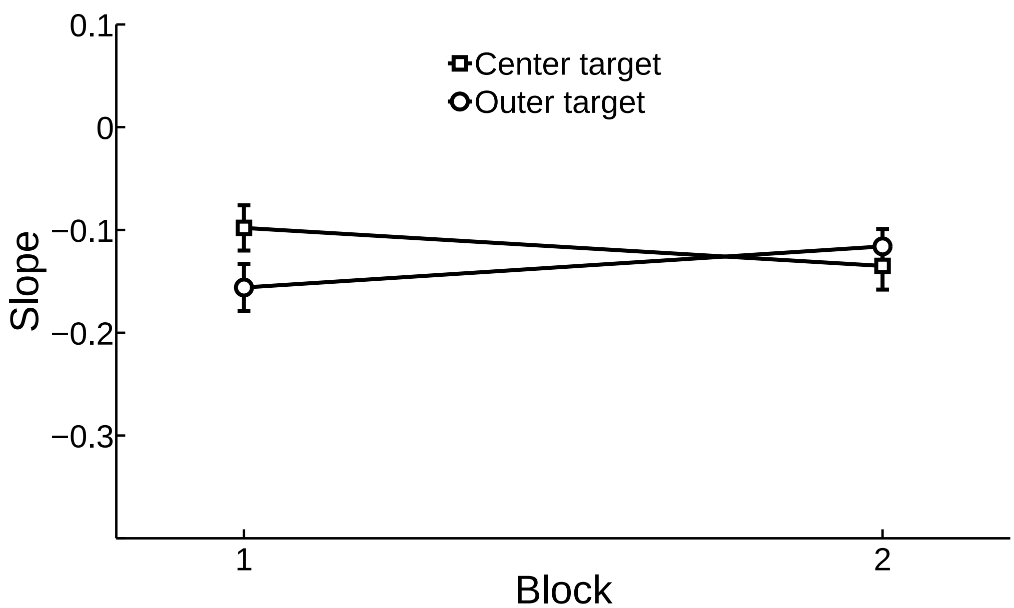

Figure 2.8: Slope values of the best-fitting straight lines for the center target (squares) and outer target (circles) as a function of block in Experiment 2. Error bars represent standard errors between subjects.

Cross-experiment analysis To directly compare initial grasp posture selection between Experiment 1 and 2, we conducted a mixed-effects ANOVA on the slopes, using block (block 1, block 2) and target (temporally proximal, temporally distal) as within-subject factors, and experiment (Experiment 1, Experiment 2) as the between-subject factor. Averaged across experiments, the temporally proximal target (mean slope = -0.201) yielded a stronger influence on initial grasp postures than the temporally distal target [mean slope = -0.076, $F(1,40) = 76.107$, $p < 0.001$, $\eta^2_p = 0.655$]. However, this effect was modulated by the significant target $\times$ experiment interaction, $F(1,40) = 54.585$, $p < 0.001$, $\eta^2_p = 0.577$. Post hoc tests indicated that the influence of the temporally proximal target was stronger in Experiment 1 (center target mean slope = -0.266) compared to Experiment 2 (outer target mean slope = -0.136, $p < 0.001$). In contrast, the influence of the temporally distal target was stronger in Experiment 2 (center target mean slope = -0.117) compared to Experiment 1 (outer target slope = -0.036, $p = 0.002$, see Figure 2.9).

2.4.3 Discussion

As in Experiment 1, MIT, AT, and initial grasp postures were influenced by both the center and the outer target indicating that participants planned the movement sequence holistically in advance. However, averaged across both experiments, the temporally proximal target had a considerably stronger influence on initial grasp postures. The stronger influence of targets that occurred proximally in an action sequence (Experiment 1: center targets, Experiment 2: outer targets) supports the planning gradient hypothesis, indicating that limitations in multi-segment grasp posture planning are driven by cognitive limitations (e.g., working memory capacity). However, cognitive limitations associated with advance planning alone do not fully account for the results of Experiment 2. Specifically, the center target (temporally distal target) also had a moderate influence on initial

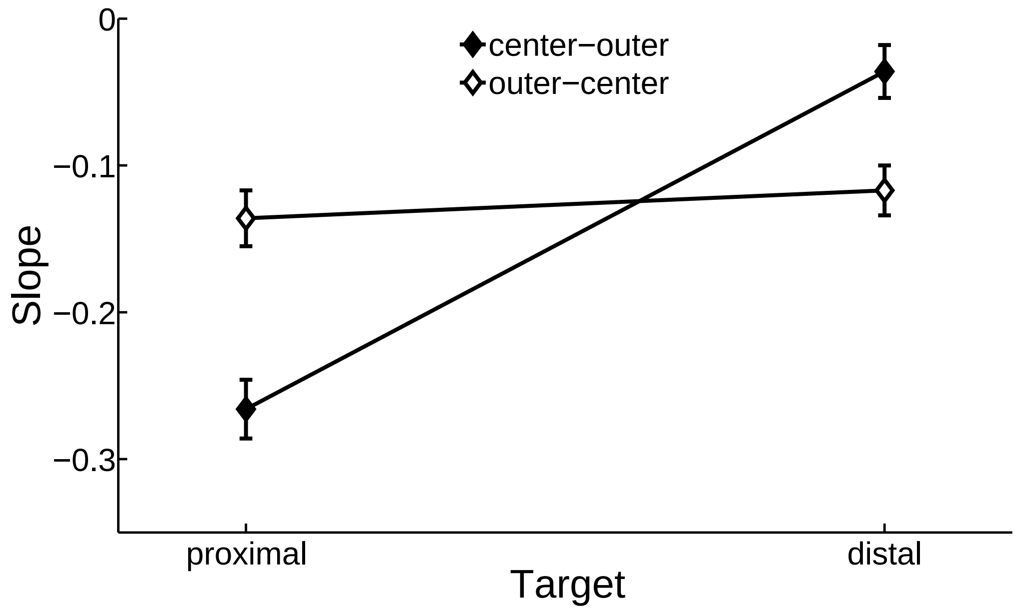

Figure 2.9: Slope values of the best-fitting straight lines as a function of target order (temporally proximal target, temporally distal target). Black diamond represent slopes from Experiment 1 (i.e., center target to outer target sequences), white diamonds represent slopes from Experiment 2 (i.e., outer target to center target sequences). Error bars represent standard errors between subjects.

grasp postures that was greater than the influence of the temporally distal target (outer target) in Experiment 1. Moreover, the findings indicate that biomechanical factors of the motor system were considered to a stronger degree (cognitive limitations could be overcome) in later repetitions, as evidenced by the increased influence of the center target and decreased influence of the outer target over repetitions. Taken together, these results demonstrate that both biomechanical factors and cognitive limitations contributed to the planning of initial grasp postures during the multi-segment movement sequences. They, however, do not provide information about the precise magnitude of the influence of each factor. Further research is needed to specify the relative contributions of these factors.

2.5 General discussion

The present study examined adaptations in initial grasp posture planning during a multi-segment object manipulation task. In line with previous work (Haggard, 1998; Hesse & Deubel, 2010), we found that initial grasp postures were influenced by the specific requirements of the temporally proximal and distal target during three-segment sequences. Replicating and extending previous work (Zhang & Rosenbaum, 2008), initial hand angles in the present study were not only inversely related to the temporally proximal, but also to the temporally distal target orientation, suggesting that participants generated movement plans that allowed them to adopt postures that optimize control at both the temporally proximal and distal segments in the action sequence.

Interestingly, initial grasp postures were differently adjusted to the requirements of the center and outer target positions, and also changed differently over the experimental session, depending on the temporal order of the targets. Averaged across both experiments, the temporally proximal target exhibited a significantly stronger influence on initial hand angle than the temporally distal target. More specifically, in Experiment 1, the center targets (temporally proximal) had a much stronger influence on initial grasp postures compared to the outer targets (temporally distal), indicating that participants prioritized control at the center target location, over control at the outer target location. In contrast, Experiment 2 revealed that outer targets (temporally proximal) had (initially) a stronger influence on initial grasp posture compared to the center target (temporally distal). The reversal of the temporal order of target location in Experiment 2 demonstrates that initial grasp postures were adjusted more to the temporally proximal, than the temporally distal, action segment. These finding support the planning gradient hypothesis (Haggard, 1998). Theoretically, improved planning for temporally proximal action segments might be one way that the CNS copes with cognitive demands associated with multi-segment action sequences.

Although limitations in planning for multiple action segments prior to movement initiation certainly influenced grasp posture planning, they cannot fully account for the results. The influence of the temporally proximal (i.e., center) target on initial grasp postures in Experiment 1 was much stronger than the influence of the temporally proximal (i.e., outer) target in Experiment 2, whereas the influence of the temporally distal target was stronger in Experiment 2 (i.e., center target) than in Experiment 1 (i.e., outer target). It is possible that differences in the number of possible target orientations between center and outer target contributed to our findings. This interpretation is further supported by the MIT and AT data. Specifically, average MIT values were much larger during Experiment 2 (2181 ms) compared to Experiment 1 (767 ms). It has been shown that the response latency increases as the amount of possible choice alternatives increases (Hick, 1952; Hyman, 1953). Recall that there were two different center target orientations, but four outer target orientations. Thus, the greater number of target orientations at the first target orientation in Experiment 2 may have increased the cognitive costs associated with the planning of initial grasp postures.

However, it is also possible that biomechanical costs associated with the spatial position of the targets account for stronger influence of the center target. Consequently, we postulate that both biomechanical and cognitive factors are considered during grasp posture planning. Support for an interaction between biomechanical factors and cognitive limitations can be derived from the changes in initial grasp postures across the experimental session. In Experiment 1, the steepness of the slopes was similar between block 1 and block 2 for both the temporally proximal (center) and the temporally distal (outer) target, indicating no adjustment of initial grasp postures to the target positions. The planning gradient hypothesis would have predicted a similar pattern for Experiment 2. This was not the case, however. During the first block of the experimental session the influence of the temporally proximal (outer) target on initial grasp postures was larger than the influence of the temporally distal (center) target. In contrast, during the second block, this difference was abolished as the influence of the temporally distal (center) target increased whereas the influence of the temporally proximal (outer) target decreased.

We speculate that the absence of adaptation in initial grasp postures in Experiment 1 result from the different weighting of the biomechanical costs associated with the spatial position and cognitive limitations in advance planning. It is likely that the biomechanical costs are considerably higher at the center target compared to the outer target position because the range of optimal control is much smaller at the center target position. Due to a planning gradient, initial grasp postures are primarily adjusted to the center target when the center target is the temporally proximal target (Experiment 1). Nevertheless, grasp postures at the outer target might still be tolerable given the larger range of optimal control at these positions. Consequently, participants did not change their grasp posture planning across several repetitions. In contrast, in Experiment 2, grasp postures are initially primarily adjusted to the outer target (temporally proximal) position. However, this resulted in grasp postures at the center target that were outside the tolerable range. Consequently, participants changed their grasp posture plans over the experimental session to better incorporate the task demands of the center target. These results suggest that there are limitations in the ability of the CNS to consider temporally distal action segments during the early stages of a task. However, over time participants learn to integrate the task demands of temporally distal steps into their movement plan, which reduces the burden on the CNS.

Together, these findings demonstrate that planning of initial grasp postures during multi-segment movement sequences is influenced by both cognitive and biomechanical factors, and that the relative influence of these constraints relies on a flexible hierarchy (see Hughes & Franz, 2008; van der Wel & Rosenbaum, 2010, for similar arguments based on experiments on bimanual grasp posture planning) that allows for adaptations in grasp posture planning over time.

Finally, it is noteworthy that action sequence length and the required degree of object rotation also affected the time to select an initial grasp posture. In line with previous work (see Christina, 1992; Fischman, Christina, & Anson, 2008; Klapp, 2010 for reviews), we found that movement initiation time and approach time was influenced by the number of steps in the action sequence, such that MIT and AT values were larger for three-segment movement sequences, compared to both one- and two-segment movement sequences. MITs and ATs also increased with the required degree of object rotation between the first and the second target. We hypothesize that anticipatory movement planning was, in part, influenced by motor imagery (e.g., Jeannerod, 1997). Similar to visual imagery (e.g., Shepard & Cooper, 1982; Shepard & Metzler, 1971), motor imagery involves mentally simulating a forthcoming action. However, in contrast to visual imagery, motor imagery is sensitive to both cognitive and biomechanical constraints (Johnson, 2000). For example, Johnson (2000) had participants reach out and grasp a dowel oriented in different ways in real space or verbally judge how they would grasp the presented dowel. The results showed that reaction time was larger for awkward hand postures, and that reaction time increased as a function of the angular distance between the initial posture and the posture chosen to grasp the dowel for both the grip and the judge condition. In line with this research, we postulate that participants mentally simulated the forthcoming actions when planning their initial grasp postures. Consequently the costs associated with multi-segment action planning increase with the number of action steps and the required degree of rotation between the first and second target, thus making it harder for participants to use motor imagery for grasp posture planning.

In sum, the results of the present study provide further evidence that multi-segment manual action sequences are planned holistically in advance. Overall, participants selected initial grasp postures based on the specific requirements of the temporally proximal and temporally distal targets, indicating that each element was considered when planning an action sequence. Interestingly, initial grasp postures were differently adjusted to the requirements of the targets depending on the temporal order in which in object was to be placed to these targets, suggesting that both biomechanical and cognitive factors influence the planning of initial grasp postures during multi-segment movement sequences. Further, the planning of initial grasp postures was influenced to a larger extent by the temporally proximal target demands during the initial stages of the experimental session. This finding suggests that cognitive limitations influence the ability of the CNS to plan for temporally distal task demands. However, with several repetitions, participants could overcome these cognitive limitations and consequently adjusted their initial grasp postures more strongly to the requirements of the temporally distal target.

Author contributions

Conceived and designed the experiments: CS, CMLH. Performed the experiments: CS. Analyzed the data: CS. Contributed reagents/ materials/ analysis tools: CS, AK, TS. Wrote the manuscript: CS, CMLH.

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3 Planning for later comfort vs. planning for minimization of postural transitions: the interplay of action selection constraints during multi-segment object manipulation tasks

This chapter is a revised version of Seegelke, C., Hughes, C. M. L., Knoblauch, A., & Schack, T. (under review). Planning for later comfort vs. planning for minimization of postural transitions: the interplay of action selection constraints during multi-segment object manipulation tasks. *Experimental Brain Research*.

3.1 Abstract

The present experiment examined the interplay of two action selection constraints during a three-segment object manipulation task: the tendency to select grasp postures that allow for comfortable or easy-to-control postures at later stages (i.e., intermediate-state and end-state comfort) and the tendency to minimize transitions between immediately forthcoming and subsequent postures. Participants grasped a cylindrical object from a home position, placed it at an intermediate position in a freely chosen orientation, and subsequently placed it at one of four final target positions. Considerable inter-individual differences in initial grasp selection were observed which also led to differences in final grasp postures. Whereas some participants strongly adjusted their initial grasp postures to the final target orientation, and thus showed a preference for end-state comfort, other participants showed virtually no adjustment in initial grasp postures and minimized postural transition between initial and intermediate grasp postures. Interestingly, as intermediate grasp postures were similar regardless of initial grasp adjustment, intermediate-state comfort was prioritized by all participants. These results provide further evidence for the interaction of multiple action selection constraints in grasp posture planning during multi-segment object manipulation tasks. Whereas some constraints may take strict precedence in a given task, other constraints may be more flexible and weighted differently among participants. This differentiated weighting leads to task- and subject-specific constraint hierarchies, and is reflected in inter-individual differences in grasp selection.

3.2 Introduction

More than 50 years ago, Napier stated that ”during the performance of a purposive prehensile action [. . .], it is the nature of the intended activity that finally influences the pattern of the grip” (1956). Said another way, what an individual plans to do with an object can be inferred from the way that the object is initially grasped. Since Napier's seminal work, several researchers have largely confirmed this assumption and shown that initial grasp postures are strongly influenced by the action goal of the task (e.g., Herbort & Butz, 2012; Hughes, Seegelke, & Schack, 2012; Hughes, Seegelke, Spiegel, et al., 2012; Rosenbaum et al., 1990; Seegelke, Hughes, & Schack, 2011; Seegelke, Hughes, Schütz, & Schack, 2012; Zhang & Rosenbaum, 2008). For example, in Zhang and Rosenbaum (2008), participants performed an object sliding task in which they placed their hand on top of an object and moved it from a start position to one of five target positions. The authors found that initial hand orientation was inversely related to final hand orientation, indicating that participants selected initial grasp postures that afforded more control when the object was moved to the target position (i.e., end-state comfort effect). The end-state comfort effect has been reliably reproduced during a variety of unimanual object manipulation tasks that require second-order planning (i.e., grasping an object and one subsequent displacement, see Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012), indicating that initial grasp postures are selected in anticipation of future goal postures, and that actions are represented in terms of goal-states (see Schütz-Bosbach & Prinz, 2007, for a review).

Since the original report demonstrating that the end-state comfort effect is a prominent constraint in grasp selection (Rosenbaum et al., 1990), subsequent research has elucidated a number of factors that influence grasp selection in second-order planning tasks. Specifically, the tendency to grasp object in a way that afford comfortable or easy-to-control final postures has been contrasted with other constraints such as the tendency to re-use previously performed actions (i.e., sequential effects, e.g., Cohen & Rosenbaum, 2004, 2011; Schütz & Schack, 2013; Schütz, Weigelt, Oderken, Klein-Soetebier, & Schack, 2011), the tendency to manipulate object with the dominant hand (Coelho, Studenka, & Rosenbaum, in press), or the tendency for the hands to stay spatially coupled during bimanual object manipulation tasks (e.g., Fischman, Stodden, & Lehmann, 2003; Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; Hughes, Reißig, & Seegelke, 2011;

Hughes, Seegelke, Reißig, & Schütz, 2012; van der Wel & Rosenbaum, 2010; Weigelt, Kunde, & Prinz, 2006).

Until recently, however, surprisingly little work has examined action selection constraints on anticipatory grasp posture planning during tasks that require higher-order planning (i.e., multi-segment sequences; Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012; Seegelke, Hughes, Knoblauch, & Schack, 2013). In one study (Seegelke et al., 2013), participants grasped a cylindrical object from a home position, placed it at a first target position, and subsequently at a second target position. The location of the first target position was fixed and required either 90° clockwise or counterclockwise object rotation (with respect to the home position). The second target positions were arranged in a semi-circular fashion around the first target position and required 0°, 45°, 135°, or 180° object rotation between the first and second target position. The authors found that initial grasp postures were inversely related to grasp postures at both the first and second target position, suggesting that participants selected grasp postures that allowed them to optimize control not only at the first (i.e., intermediate-state comfort), but also at the second, target position (i.e., end-state comfort). Additionally, Seegelke et al. (2013) found that initial grasp selection depended on the temporal order of the targets, such that grasp postures were more strongly adjusted to the requirements of the first, rather than the second, target position (i.e., a 'planning gradient'). Together these findings demonstrate that the planning of initial grasp postures during multi-segment object manipulation tasks is contingent upon biomechanical (comfort or control at later stages) as well as cognitive (i.e. planning gradient) constraints, and that the relative importance of these constraints relies on a flexibly hierarchy (Hughes & Franz, 2008; van der Wel & Rosenbaum, 2010).

Hesse and Deubel (2010) have provided further evidence that grasp posture planning extends to three-segment object manipulation sequences. In their task, participants reached and grasped a cylinder, placed it on a target circle, and subsequently grasped and displaced a bar that was positioned in one of three orientations. The authors found that the orientation of the bar at the end of the movement sequence influenced the grip orientation that participants used when grasping the cylinder, and that grip orientation in these early movement segments was systematically shifted towards the final grip orientation (i.e., when grasping the bar). It has been argued that this shift reflects the tendency of the central nervous system to minimize transitions between immediately forthcoming postures and subsequent postures (Rosenbaum, Chapman, Coelho, Gong, & Studenka, 2013), and hence is an influential constraint in tasks that require higher-order planning (see also Studenka, Seegelke, Schütz, & Schack, 2012, for similar results).

The aim of the present study was to examine the interplay between tendency to select grasp postures that allow for comfortable or easy-to-control postures at later stages (i.e., intermediate- and end-state comfort, e.g., Rosenbaum et al., 1990; Seegelke et al., 2013) and the tendency to minimize differences between immediately forthcoming and subsequent postures (Hesse & Deubel, 2010; Rosenbaum et al., 2013; Studenka et al., 2012) during a multi-segment object manipulation task. To this end, we modified the three-segment object manipulation task used in Seegelke et al. (2013) such that the object orientation at the first (intermediate) target position was unconstrained and participants were free to place the object in any desired orientation (similar as in Hesse & Deubel, 2010). Thus, participants grasped a cylindrical object from a home position, placed it at an intermediate target position in a freely chosen orientation, and subsequently placed it at one of four final target positions in a predetermined orientation.

We expected that initial grasp postures should be inversely related to final grasp postures if end-state comfort is the predominant factor in the grasp planning hierarchy. Further, given that the object could be placed in any desired orientation at the intermediate target position, evidence for intermediate-state comfort dominance would be indicated if participants adopted similar intermediate grasp postures (i.e., comfortable or easy-to-control postures) regardless of initial grasp posture adjustment and final target orientation. In contrast, if minimizing postural transitions is the dominant grasp planning constraint, we entertained the following possibilities: First, if participants minimized postural differences between initial and intermediate grasp postures, initial and intermediate grasp postures should be similar. Second, if participants minimized postural transition between intermediate and final grasp postures, intermediate and final grasp postures should be similar. Finally, it is also possible that there is a trade-off between minimization of postural transition of initial and intermediate grasp postures on the one hand, and minimization of postural transition of intermediate and final postures on the other hand. If this is the case, we expected that intermediate grasp posture should be steered towards final grasp postures (as in Hesse & Deubel, 2010).

3.3 Methods

3.3.1 Participants

20 individuals from Bielefeld University (5 men, 15 women, *M* age = 22.70 years, *SD* = 3.16) participated in exchange for 5 € compensation. All participants were right-handed (*M* score = 99.35, *SD* = 2.91) as assessed using the Revised Edinburgh Handedness Inventory (Dragovich, 2004). Participants reported normal or corrected to normal vision, and did not have any known neuromuscular disorders. The experiment was conducted in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

3.3.2 Apparatus and stimuli

The experimental apparatus was similar to that used in a previous study (Seegelke et al., 2013) and is shown in (Figure 3.1A and 3.1B). The set-up was positioned on a height adjustable shelf (200 cm $\times$ 60 cm). The home, intermediate, and final positions consisted of white paper circles (11 cm in diameter) that were taped flat to the surface of the shelf. The home and final positions had outward extending paper protrusions (9 cm $\times$ 2 cm) and were arranged in a semi-circle, each separated by 45°. Viewed from the participant's perspective, the home position was located at 0°, while the final positions were located at -90°, -45°, 45°, and 90°. The intermediate position was a white target circle (11 cm in diameter) and was located midway between the -90° and 90° final targets. The manipulated object was a grey PVC cylinder (5 cm in height, 10 cm in diameter) with a protrusion (8.5 cm × 1 cm) that extended from the bottom of the object (Figure 3.1C).

Visual stimuli were presented on a 127 cm flat screen Monitor (Panasonic TH-50PF11EK) that was placed behind the shelf. The stimuli consisted of a visual representation of the set-up (bird's eye view) and displayed the required final target position (Figure 3.1A). Stimulus presentation was controlled via Presentation®(Neurobehavioral Systems).

Kinematic data was collected from three retro reflective markers (14 mm in diameter) placed dorsally on the distal end of the third metacarpal (MCP), the styloid process of the ulna (WRP), and the styloid process of the radius (WRT) of the right hand. Two markers (10 mm in diameter) were placed on the object protrusion (5 cm [PP] and 0.5 cm [PD] from the tip of the protrusion,(Figure 3.1C). Kinematic data was recorded using an optical motion capture system (VICON Motion Systems, Oxford, UK) consisting of 10 Bonita cameras with 200 Hz temporal and 1 mm spatial resolution.

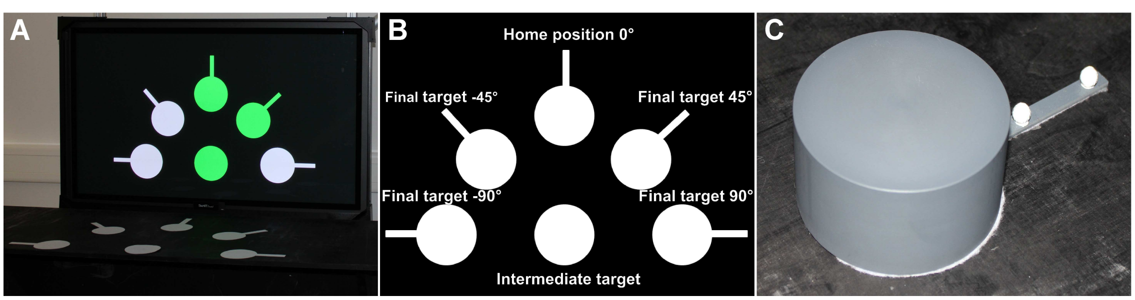

Figure 3.1: Experimental setup and stimuli. A Front view of the experimental setup. Exemplary stimulus indicating a sequence in which the object is to be placed to the 45° final target. B Top view of the experimental setup including target labels. C Manipulated object.

3.3.3 Procedure

After entering the lab, participants filled out the informed consent and handedness inventory. Participants arm length and hip height was measured, and the markers were placed on the right hand. The shelf was adjusted to hip height and the home and target circles were arranged so that their distance from the intermediate target was 60 % of the participant's arm length. The participant stood in front of the experimental setup so that the right shoulder vertically coincided with the home and intermediate target position.

At the beginning of each trial, the experimenter placed the object on the home position. The message "Put your hand to the start position!" (in German) was displayed on the monitor, and the participant placed the hand on the shelf 10 cm to the right of the intermediate target with the fingers pointing up (12 o'clock position). A fixation cross was then displayed for 500 ms, and after a random time interval (500 - 1500 ms), the stimulus was presented for 500 ms. When the stimulus appeared, the participant grasped the object from the home position, placed it at the intermediate position, and then at the final target position, as indicated by the stimulus. The participant then brought the hand back to the start position and waited for the next trial to begin.

The orientation of the object at the intermediate position was not prescribed, but could be freely chosen by the participant. Participants were told to grasp the object by placing their palm on top of the object so that the fingers were arranged around the sides of the cylinder, and not to change the selected grasp throughout the trial. The instructions also emphasized that the task should be performed at a comfortable speed, and movement accuracy was stressed. Each final target was presented ten times in a randomized order, yielding a total of 40 trials. A session lasted about 30 minutes.

3.3.4 Data Analysis

The 3D coordinates of the retro-reflective markers were reconstructed and labeled. Any missing data (less than 10 frames) were interpolated using a cubic spline and filtering using a Woltring filter (Woltring, 1986) with a predicted mean square error value of 5 mm^2 (Vicon Nexus 1.7)[1]. Kinematic variables were calculated using a custom written MatLab program (The MathWorks, Version R2010a). The wrist joint center (WJC) was calculated as the midpoint between WRT and WRP. In addition, two direction vectors were calculated, one pointing distally from the WJC to MCP (V1 = MCP - WJC), and a second one passing through the wrist (V2 = WRP - WRT). The hand center (HC) was defined on a plane normal to $V1 \times (V2 \times V1)$, positioned palmar from MCP at a distance of 19.5 mm which corresponds to (average hand thickness + marker diameter)/2 in a way that (HC – WJC) and (HC – MCP) formed a right angle (Figure 3.2A). The hand angle was calculated as the projection of the vector pointing distally from WJC to HC on the shelf plane (Figure 3.2B). Thus, hand orientations with the fingers pointing up (12 o'clock position), left (9 o'clock position), right (3 o'clock position), and down (6 o'clock position) would result in hand angles of 0°, -90°, 90°, and 180°, respectively. Similarly, the object orientation angle was calculated as the projection of the vector pointing distally from PP to PD on the shelf plane.

[1] The Woltring filter is commonly used in the analysis of motion capture data and is equivalent to a double Butterworth filter. The benefit to the Woltring filter is that higher-order derivates can be calculated from the analytic derivative of a polynominal spline.

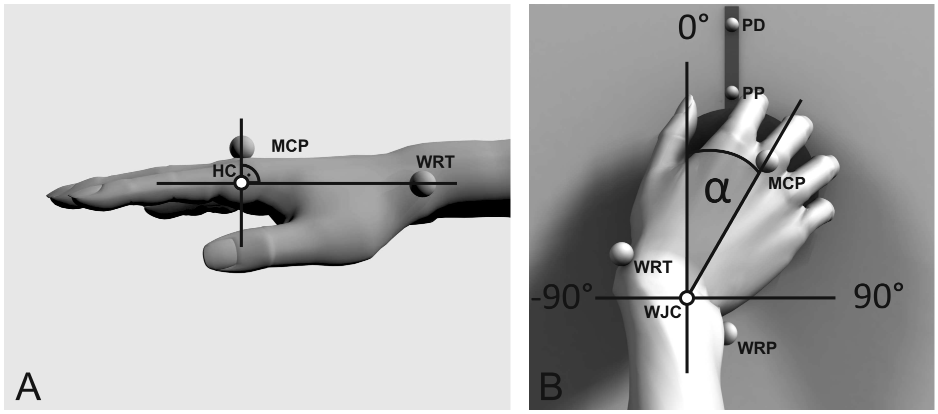

Figure 3.2: Calculation of HC (panel A) and hand orientation angle α (panel B).

For each trial, the time series was divided into three movement segments. The initial movement segment was defined as the time period between when the hand left the start position to the time period when the hand grasped the object. The intermediate movement segment was defined as the time period between when the object was lifted from the home position to the time period when the object was placed to the intermediate target position. The final movement segment was defined as the time period when the object was lifted from the intermediate target position to the time period when the object was placed to the final target position.

Movement onset of each segment was determined as the time of the sample in which the resultant velocity of the hand (WJC) exceeded 5 % of peak velocity of the corresponding phase. Movement offset was determined as the time of the sample in which the resultant velocity dropped and stayed below 5 % of peak velocity of the corresponding phase. Initial, intermediate, and final hand and object orientation angles were extracted at movement offset of the corresponding segment.

Trials performed in a non-instructed manner (e.g., moving prior to stimulus presentation, placing the object to a wrong target, changing the grasp during a trial) were counted as errors and were not included in analysis. Error trials comprised less than 1 % of the data, and were approximately equally distributed across condition.

3.4 Results

Mean initial hand orientation angles were 6.5°, 3.7°, -10.2°, and -18.1° and inversely related to the corresponding final hand orientation angles -78.7°, -39.7°, 25.7°, and 55.3° (for the final target positions -90°, -45°, 45°, and 90° respectively)[2]. A repeated measures analysis of variance (RM ANOVA) with the factors repetition (1-10) and final target position (-90°, -45°, 45°, 90°) confirmed that the effect of final target position on initial hand orientation angle was significant, $F(3,57) = 20.616$, $p < 0.001$ (see Figure 3.3). The main effect of repetition and the final target $\times$ repetition interaction were not significant (both $p > 0.05$).

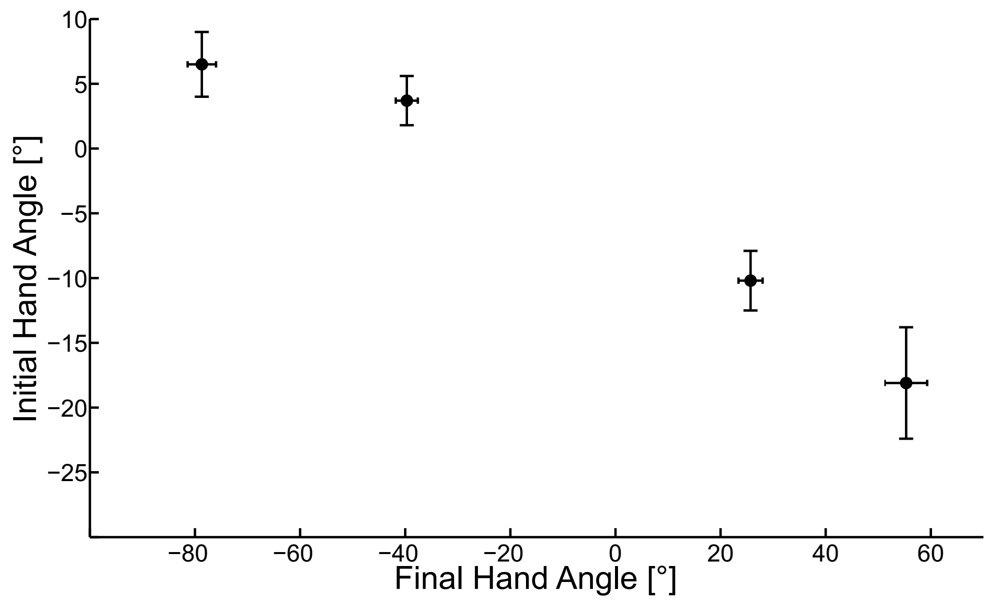

Figure 3.3: Mean initial hand angle (± 1SE) and corresponding mean final hand angle (± 1SE).

To examine the extent to which intermediate hand and/or object orientation angles (i.e.,

[2]The difference between initial and final hand orientation angle does not fully correspond to the required degree of object rotation. As participants did not readjust their initial hand orientation, it is likely that grasp adjustments also involved changing the point of contact on the object by a subset of fingers (Haggard, 1998).

grasp-object configuration) were adjusted to the final target positions, a repeated measures multivariate analysis of variance (RM MANOVA) with the factors repetition and final target position and the intermediate hand and object orientation angles as dependent variables was performed . Analysis revealed that final target position influenced the grasp-object configuration at the intermediate target position, $F(6,14) = 3.970$, $p = 0.016$. Again, neither the main effect of repetition, nor the final target × repetition interaction, was significant (both $p > 0.05$). Follow-up univariate ANOVAs indicated that mean intermediate object orientation angles (-25.0°, -13.4°, 10.4°, 20.8°) were systematically shifted towards the corresponding final object orientation angles -91.1°, -46.5°, 44.4°, and 88.5°, respectively, $F(3,57) = 12.095$, $p = 0.002$ (Figure 3.4B).

Post hoc tests confirmed that all comparisons were significant (all $p < 0.05$). In contrast, mean intermediate hand orientation angles (-18.5°, -13.0°, -9.9°, -9.4°) were similar regardless of final target position, $F(3,57) = 2.447$, $p = 0.132$ (Figure 3.4A).

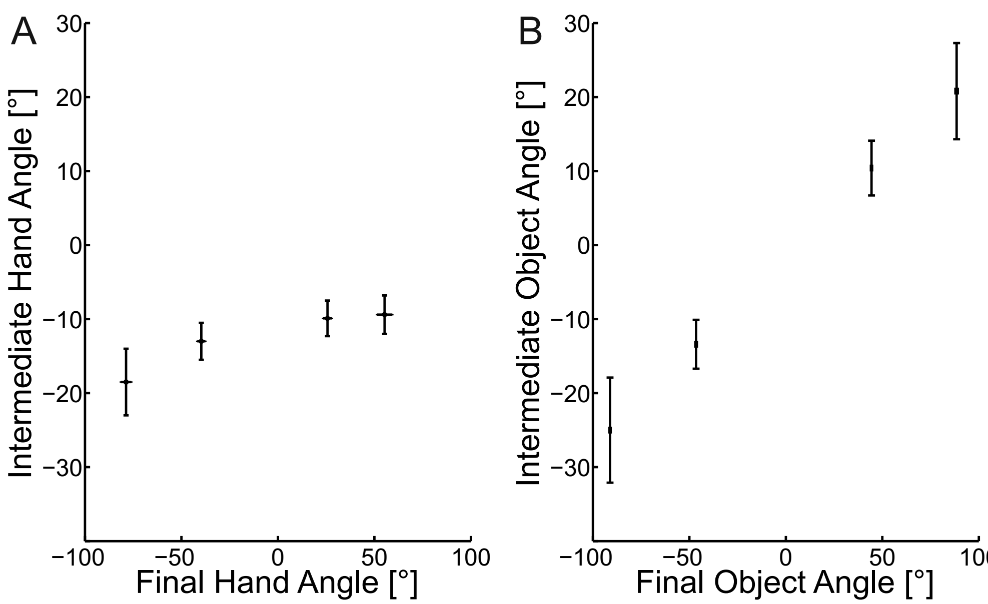

Figure 3.4: A Mean intermediate hand angle (± 1SE) and corresponding mean final hand angle (± 1SE) B Mean intermediate object angle (± 1SE) and corresponding mean final object angle (± 1SE).

Closer inspection of the data revealed inter-individual differences in the adjustment of initial grasp postures. To examine the magnitude of differences in initial grasp posture adjustment, we conducted linear regressions for the initial hand angles on the final target positions, separately for each participant. The slopes of these regressions provide an estimate of the degree of initial grasp posture adjustment and ranged from 0.000 (no adjustment) to -0.429 (strong adjustment). Given that object orientation at the final target positions was predetermined these differences resulted in differences in the corresponding final grasp postures (see Figure 3.5). To examine whether a strong adjustment in initial grasp postures would result in more controllable (or comfortable) final grasp postures, we compared the final grasp postures from the present experiment with the most comfortable postures at each of the four final target positions[3]. To this end, we first calculated the deviation of the final grasp postures from the corresponding average comfortable grasp postures separately for each participant and final target position. We then averaged these values across all final target positions and correlated them with participants' slopes of initial grasp posture adjustment. Analysis revealed a significant correlation (r = 0.683, p = 0.001) indicating that prospective planning for more comfortable (or controllable) final grasp postures resulted in a strong adjustment in initial grasp posture.

[3]To quantify comfortable grasp postures, we obtained an independent measure of grasp comfort at each position (i.e., home position, intermediate target position, final target positions -90°, -45°, 45°, and 90°) using a separate pool of participants (n = 15, *M* age = 25.60, *SD* = 4.08, 10 women, 4 men). The experimental setup and motion capture analysis were identical to that used in the main experiment. At the start of each trial, the experimenter placed the object on a target position, and participants were told to reach out with their right hand and grasp the object with the most comfortable grasp posture. Participants then placed their hand back to the side of the body and waited for the next trial to begin. Each position was repeated five times in a randomized order yielding a total of 30 trials.

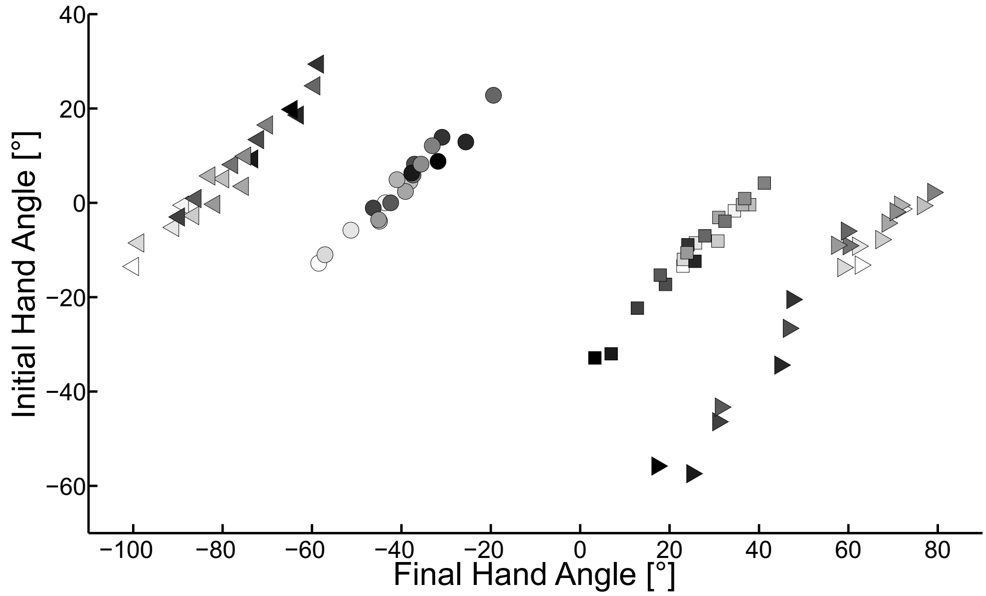

Figure 3.5: Scatter plot comparing initial hand angles with corresponding final hand orientation angles for the final target position -90° (left pointing triangle), -45° (dots), 45° (squares), and 90° (right pointing triangles). Each symbol color corresponds to a single participant. The shade of the symbols represent the participants' degree of adjustment in initial grasp posture, such that increasing darkness of the symbols represent increasing steepness of the slopes.

Given that participants were free to select the orientation of the object at the intermediate target position, we also examined whether inter-individual differences in initial grasp posture adjustment would be reflected in the intermediate hand and object orientation angles. To this end, we evaluated the influence of initial grasp selection on intermediate grasp postures and/or intermediate object orientation by calculating 1) correlations between initial hand orientation angles and intermediate hand orientation angles and 2) correlations between initial hand orientation angles and intermediate object orientation angles (see Figure 3.6).

Analysis revealed moderate (-90° = -0.50, -45° = -0.49, 45° = -0.62) to strong negative correlations (90° = -0.87, Figure 3.6B) between initial hand orientation and intermediate object orientation angle, all $p < 0.05$. In contrast, there was no significantly observable linear relationship between initial hand orientation angle and intermediate hand orientation angles (-90° = -0.01, -45° = 0.36, 45° = 0.26, 90° = 0.00, all $p > 0.120$, Figure 3.6A)[4]. Thus, the inter-individual differences in initial grasp choice were manifest in intermediate object placement (i.e., strong initial grasp adjustments resulted in large intermediate object adjustments) whereas intermediate grasp posture remained relatively invariant regardless of the strength of initial grasp adjustment.

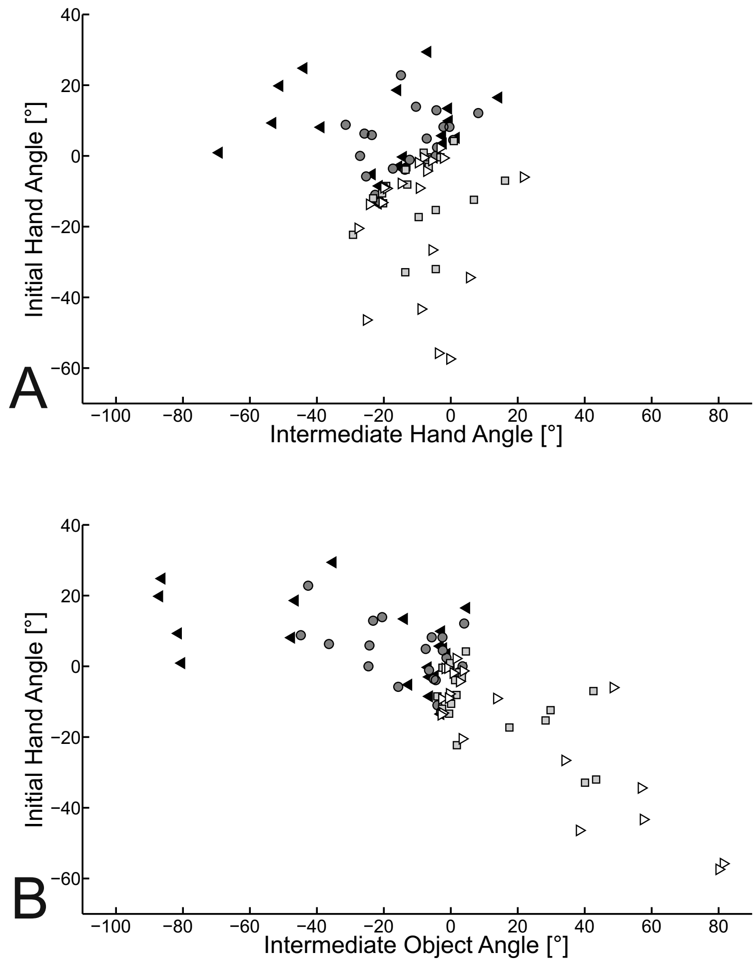

Figure 3.6: A Initial hand orientation angles with corresponding intermediate hand orientation angles and B corresponding intermediate object orientation angels for the final target positions -90° (left pointing triangle), -45° (dots), 45° (squares), and 90° (right pointing triangles).

[4]Mean intermediate hand orientation angles were -19.2°, -13.0°, -9.9°, and -9.4° for final target positions -90°, -45°, 45°, and 90° and thus, very similar to the most comfortable intermediate hand orientation angle (-13.4°).

3.5 Discussion

The present study explored the relative importance of intermediate-state and end-state comfort (i.e., the tendency to select grasps that afford comfortable and controllable postures at later stages in the task; Rosenbaum et al., 1990; Seegelke et al., 2013) and the tendency to minimize transitions between immediately forthcoming and subsequent postures (Hesse & Deubel, 2010; Rosenbaum et al., 2013; Studenka et al., 2012) during an object manipulation task that required higher-order planning.

In general, our results suggest that participants, when planning their initial grasp postures during multi-segment object manipulation tasks, prioritize later comfort or control, rather than minimizing postural transitions between forthcoming postures. Complementing previous work (Seegelke et al., 2013; Zhang & Rosenbaum, 2008), average initial hand orientation angles were inversely related to final hand orientation angles. This finding indicates that participants planned the manual action sequence such that they adopted initial grasp postures that afford comfortable or easy-to-control grasp postures at the end of the sequence (i.e., end-state comfort). In addition, intermediate hand orientation angles were not influenced by the final target orientation, and highly similar to the most comfortable hand orientation angles derived from the comfort ratings. In contrast, intermediate object orientation was influenced by the final target positions, such that when placing the object at the intermediate target position, the orientation of the object protrusion was shifted towards the final target orientation. Thus, these findings provide further evidence that participants prioritized comfort at the end, as well as at the middle, of the action sequence, and reinforce prior work indicating that end-state comfort is a predominant constraint in action selection.

These findings certainly indicate that selecting initial grasp posture that allow for comfort at later stages is weighted higher than the tendency to minimize postural transitions. However, closer inspection of the data revealed the presence of inter-individual differences in initial grasp posture selection, ranging from very strong adjustment to virtually no adjustment (which also resulted in individual differences in final grasp postures). Importantly, we also found that intermediate grasp postures were relatively similar between participants (and therefore similar to most comfortable intermediate postures), independent of initial grasp posture adjustment. In contrast, intermediate object orientation was strongly related to initial grasp postures, and thus influenced by the final target position. Specifically, we observed moderate to strong negative correlations between initial hand orientation angles and intermediate object orientation angles, but only weak correlations between initial hand orientation angles and intermediate hand orientation angles.

These findings complement the growing body of evidence that have reported inter-individual differences in initial grasp posture planning during unimanual (Hughes, Seegelke, & Schack, 2012; Rosenbaum, van Heugten, & Caldwell, 1996; Seegelke, Hughes, Schütz, & Schack, 2012) and bimanual object manipulation tasks (Fischman, Stodden, & Lehmann, 2003; Hughes & Franz, 2008; Hughes, Seegelke, Reißig, & Schütz, 2012), and add to the framework of action selection outlined in previous work from our laboratory (Hughes & Franz, 2008; Hughes, Haddad, et al., 2011; Hughes, Seegelke, Reißig, & Schütz, 2012; Hughes, Seegelke, & Schack, 2012; Seegelke et al., 2011, 2012). According to this framework there exists a flexible action selection constraint hierarchy in the central nervous system which is guided by the action goals of the task. Optimally the decision maker seeks to simultaneously satisfy the task goals as well as action constraints. The selection of appropriate grasp postures, thus, is contingent upon the higher level action goals of the task and the lower level action constraints. In situations in which optimal decision making is not possible, the constraints are given weight factors, and ordered hierarchically according to their importance. The relative weighting of these constraints not only depends on the action goals of the task, but also upon contextual, conceptual, environmental, and internal influences. In addition, different weights can also be assigned to the action goal. On the one hand, if the action goal of the task is highly important, the weight factor of the constraints will be reduced to a larger degree in order to increase the action goal function (i.e., likelihood of successful goal attainment, i.e., top-down mechanisms). On the other hand, increasing the weight factor of a given constraint can also affect action goal accomplishment (i.e., bottom-up mechanisms). According to this view, inter-individual differences in task performance are a result of variations in the relative order of action selection constraints between individuals (Hughes, Haddad, et al., 2011; Seegelke et al., 2011, 2012).

Based on the theoretical considerations of this framework, it follows that the associated weight factors of the two action selection constraints (end-state comfort and minimizing postural transitions between forthcoming postures) differed between individuals. In the present task, strong adjustments in initial grasp posture led to more comfortable (or controllable) final postures, whereas small or no adjustments resulted in less comfortable or even awkward final postures. Consequently, it is likely that participants who strongly adjusted their initial grasp postures weighted the tendency to adopt postures that allow for later control higher than the tendency to minimize postural differences.

The question can be asked as to whether there is evidence indicating that individuals who did not adjust (or exhibited a small degree of initial grasp posture to the final target position adjustments) gave a higher weight function to the minimizing postural transitions constraint. Our data demonstrate that participants did not attempt to minimize postural transitions between intermediate and final grasp postures, as intermediate hand orientation was not biased towards final hand orientation. However, the data indicate that these participants minimized postural transitions at early action segments (i.e., between initial and intermediate grasp postures). By selecting similar initial and intermediate grasp postures, these participants might not have only reduced the cognitive costs associated with grasp posture planning by selecting similar initial grasps regardless of final target position (see Hughes, Seegelke, Reißig, & Schütz, 2012), but also assured to adopt comfortable intermediate postures, suggesting that these participants considered intermediate-state comfort as well.

The relative invariance of intermediate grasp postures regardless of final target and individual initial grasp posture adjustments suggests that biomechanical characteristics of the arm were taken into account in the motor plan prior to movement onset (Cos, Belanger, & Cisek, 2011; Cos, Medleg, & Cisek, 2012). Specifically, it is likely that sufficient control in the present task could be obtained only by a very limited range of postures at the intermediate target position (i.e., even small changes in intermediate grasp posture would place the hand close to the extremes of the range of motion), whereas the range of optimal control is less narrow at the final target positions. Accordingly, in this task, selecting comfortable or easy-to-control intermediate grasp postures appears to be a predominant constraint which is prioritized by all participants. Given the observation that anticipatory posture adjustments are made to facilitate subsequent movements (Lakie, Caplan, & Loram, 2003; Lakie & Loram, 2006), the adoption of an invariant controllable intermediate grasp posture is likely to be a key factor in a sense that it facilitates the production of the final movement segment. Conversely, end-state comfort or minimizing postural transitions appear to be subordinate constraints in the hierarchy and their importance might be weighted differently among participants, leading to different initial and final grasp postures between participants.

In sum, the data of the present study provide further evidence that grasp posture planning is contingent upon multiple constraints that compete with each other during the selection of appropriate grasp postures. Whereas some constraints may strictly take precedence in a given task, others may be regarded more flexible and weighted differently among participants dependent on contextual, environmental, and internal influences. This differentiated weighting leads to task- and subject-specific constraint hierarchies, which in turn, are reflected in inter-individual differences in the selection of grasp postures.

Author contributions

Conceived and designed the experiments: CS, TS. Performed the experiments: CS. Analyzed the data: CS. Contributed reagents/ materials/ analysis tools: CS, AK, TS. Wrote the manuscript: CS, CMLH.

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4 Motor planning during multi-segment action sequences - extension to two-object manipulation tasks

This chapter is a revised version of Seegelke, C., Hughes, C. M. L., Schütz, C., & Schack, T. (2012). Individual differences in motor planning during a multi-segment object manipulation task. *Experimental Brain Research, 222*, 125-136.

4.1 Abstract

Research has demonstrated that people will adopt initially awkward grasps if they afford more comfortable postures at the end of the movement. This end-state comfort effect provides evidence that humans represent future posture states and select appropriate grasps in anticipation of these postures. The purpose of the study was to examine to what extent the final action goal of a task influences motor planning of preceding segments, and whether grasp postures are planned to optimize end-state comfort during a three-segment action sequence in which two objects are manipulated, and participants can select from a continuous range of possible grasp postures. In the current experiment, participants opened a drawer, grasped an object from inside the drawer, and placed it on a table in one of three target orientations (0°, 90°, or 180° object rotation required). Grasp postures during the initial movement segment (drawer opening) were not influenced by the final action goal (i.e., required target orientation). In contrast, both the intermediate (i.e., object grasping) and the final movement segment (i.e., object placing) were influenced by target orientation. In addition, participants adopted different strategies to achieve the action goal when the object required 180° rotation, with 42 % of participants prioritizing intermediate-state comfort, and 58 % prioritizing end-state comfort. The results indicate that individuals optimize task performance by selecting lower-level constraints that allow for successful completion of the action goal, and that the selection of these constraints is dependent upon contextual, environmental, and internal influences.

4.2 Introduction

A characteristic of successful motor performance is the ability to plan and execute movements so that everyday tasks can be accomplished. Although movement kinematics are highly influenced by the properties of the object, the intentions of the actor, and the goals of the task (Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Armbrüster & Spijkers, 2006; Jeannerod, 1981, 1984; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987), there is remarkable similarity in the grasp postures individuals select when manipulating objects.

The relative invariance in grasp postures was first described by Rosenbaum et al. (1990). In that study, participants grasped a horizontally arranged bar and placed either the left end or the right end of the bar into a target disc. Rosenbaum et al. (1990) found that the hand posture (overhand or underhand) used to grasp the bar depended on which end of the bar was to be inserted into the target disc - participants grasped the bar with an underhand posture when the left end of the bar was to be inserted into the target disc, and an overhand posture when the right end of the bar was to be inserted into the target disc. Stated a different way, participants always grasped the bar with an initial hand posture that ensured a comfortable posture at the end of the movement. Called the end-state comfort effect, this phenomenon indicates that future body states are represented, and that individuals select initial grasps in anticipation of these future postures.

Motivated by these findings, Haggard (1998) investigated whether grasp posture planning extends to action sequences that require multiple movements. Participants grasped an octagonal object and performed a movement sequence composing of two, three, or five action steps. The movement sequences were identical except that participants had to move the object to one of two critical target positions at the 2nd, 3rd, or 5th step in the sequence. When the movement sequences involving different target positions were compared, Haggard found that initial grasp postures differed depending on the specific movement sequence participants were instructed to perform for sequences consisting of up to three action steps. Based on these results Haggard argued that people are able to plan an appropriate initial grasp posture when the multi-sequence movement consists of two or three action steps[1]. Haggard also found that differences in initial grasp posture were more likely to occur when the critical target occurred early on in the movement sequence, which he took as evidence that early steps in an action sequence are considered more compared to later steps (i.e., a gradient of grasp posture planning).

More recent research has examined whether motor planning extends to situations in where multiple objects are manipulated (Hesse & Deubel, 2010a). In the study of Hesse and Deubel (2010a, Experiment 1) participants performed a pick-and-place action sequence that consisted of three movement segments and the manipulation of two different objects. In the first movement segment, participants reached and grasped an object (4 cm diameter cylinder) located 20 cm to the left of the hand start position, and placed the object on a target circle (second movement segment). In the third movement segment, participants grasped a second object that was positioned in one of three orientations and placed it in the middle of the workspace. The authors found that the orientation of the second object (i.e., the target bar) in the third movement segment influenced the grip orientation of the first and second movement segment (i.e., when grasping and when releasing the cylinder), suggesting that anticipatory motor planning extends to situations in which multiple objects are manipulated.

In sum, the results of Haggard (1998) and Hesse and Deubel (2010a, Experiment 1) indicate that individuals consider each element of a multi-segment action when planning their initial grasp postures, and that initial grasp postures depend critically on task requirements in the final steps of a movement sequence. However, from these two studies, it is unclear what individuals planned in advance. One possibility is that people plan their grasp postures to ensure comfort at the end of a movement. The sensitivity toward comfortable end postures has been found to generalize to a number of experimental paradigms during two segment movement sequences (i.e., grasping and placing of a single object), and

[1] When participants made adjustments to initial grasp posture, they typically did so by changing the placement of the individual fingers, rather than rotating the whole hand.

is a predominant grasp selection constraint in unimanual tasks (see Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006, for a review). But whether people plan their grasp postures to satisfy end-state comfort during an action sequence consisting of more than two segments has yet to be fully investigated. The present study built on this previous work and investigated motor planning during a multi-segment action sequence in which two objects are manipulated, and participants can select from a continuous range of possible grasp postures. Of particular interest was the extent to which the final action goal of the task influences the planning (i.e., grasp postures and movement times) of the preceding segments during a three step movement sequence, and whether grasp postures are planned to optimize comfort at the end of the movement.

To address these questions, participants were asked to perform a three segment grasping and placing action sequence. In this task, participants opened a drawer (initial movement segment), grasped a cylindrical object from inside the drawer (intermediate movement segment), and placed the object on a table (final movement segment). The final action goal of the task was manipulated such that participants placed the object on a table in one of three different target orientations (from the participants perspective: up [0° rotation], left [90° rotation], or down [180° rotation]).

Based on previous research (Haggard, 1998; Hesse & Deubel, 2010a, Experiment 1) indicating that individuals are able to plan the entire action sequence prior to movement initiation (i.e., before opening the drawer), it is expected that grasp posture and movement times during the first movement segment (i.e., drawer opening) would be influenced by the final action goal of the task (i.e., specific end orientation when placing the object on the target). However, given that participants do not have to maintain their initially selected grip during the entire action sequence, it is also possible that later movement segments would influence only the *immediately preceding*, rather than *all*, grasp postures in the movement sequence (a sequential planning strategy). That is to say, the final goal of the movement would influence the grasp posture of the intermediate, but not the initial movement segment.

Moreover, previous research has shown that people plan their grasp postures to afford comfortable end-states (e.g., Rosenbaum et al., 1990). Thus it is expected that individuals will grasp the object with a posture that results in similar final postures regardless of target orientation in the final movement segment. Thus, intermediate but not final grasp postures should differ as a function of object end orientation. However, there also exists the possibility that the ability to plan for comfortable end postures does not extend past the second segment in an action sequence. If this is the case, then it is expected that final grasp postures would differ as a function of object end orientation, but that intermediate grasp postures would be similar for all target orientations. Last, it is also possible that grasp comfort would be dispersed between the intermediate and final movement segments. If this is the case, then it is expected that both intermediate and final grasp postures would change as a function of object end orientation.

4.3 Methods

4.3.1 Grasping task

Participants 20 students from Bielefeld University took part in the experiment in exchange for experimental course credit. The data set from one participant was removed prior to analysis as the participant was unable to follow instructions. The remaining 19 participants (*M* age = 21.95, *SD* = 5.23, 3 men, 16 women) were classified as right-handed (*M* = 81.6, *SD* = 16.5) as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Participants had normal or corrected to normal vision, did not have any known neuromuscular disorders, and were naïve to the purpose of the study. The experiment was conducted in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

Apparatus Figure 4.1 shows the set up of the experiment. The apparatus consisted of a drawer ($8.5 \times 20 \times 30$ cm) attached to a wooden platform. Affixed to the center of the drawer face was a cylindrical knob (7 cm in diameter, 4 cm in height). The drawer could be adjusted to participant's hip height by sliding the wooden platform up and down on four metal poles (each 2 m in height, 2 cm in diameter).

The manipulated object was a PVC cylinder (7 cm in diameter, 4 cm in height, and 215 g in weight) with a black mark (0.5 cm in width) on top, which extended from the center to the outer edge of the object. Located inside the drawer was a 7.2 cm diameter socket (0.5 cm in depth) that served to house the object. A black mark (0.5 cm in width, 3.5 cm in length) extended from the socket toward the back of the drawer. The object was visible to the participants before the drawer was opened. At the start of each trial, the object was situated so that the marks on the object and socket coincided with one another.

The wooden target board (29 cm $\times$ 29 cm) was height adjustable, and featured a centrally located socket (7.2 cm in diameter, 0.5 cm in depth). Radiating from the outside edge of the target well were three colored marks (blue, green, and red, 0.5 cm in width, 3.5 cm in length)[2] that indicated the three target orientations up, left, and down. These target orientations required the participants to rotate the object 0°, 90°, or 180°, respectively.

Motion capture Kinematic data was recorded using an optical motion capture system (VICON Motion Systems, Oxford, UK) consisting of 12 MX-F20 CCD cameras with 200 Hz temporal and 0.25 mm spatial resolution. Retro reflective markers (14 mm in diameter) were placed dorsally on the distal end of the third metacarpal (MCP), the styloid process of the ulna (WRP), the styloid process of the radius (WRT), the medial and lateral epicondyle of the humerus (ELM and ELL respectively), the acromion process (ACR) of the right arm, the suprasternal notch (CLAV), the xiphoid process (STRN), the 7th

[2] In order to control for perceptual effects associated with target perception, the spatial arrangement of the colored marks on target board was randomized.

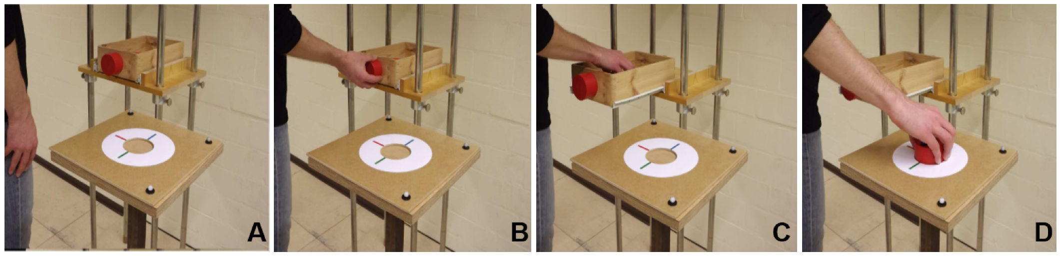

Figure 4.1: Set up and procedure of the experiment. A At the start of the trial, the participant stood with the right arm by the side of the body. B After a signal from the experimenter indicating the required target orientation of the object, the participant opened the drawer by the knob (initial movement segment), C grasped the object from inside the drawer, D placed it on the target board in the predefined target orientation.

cervical vertebra, and the 8th thoracic vertebra of the torso. In addition, a marker (10 mm in diameter) was placed on top of the object (2.5 cm from the center), and 3 markers (10 mm in diameter) were placed on the corners of the target board (top left, top right, and bottom right). These markers were used for the calculation of end orientation error (measured in degrees [°]).

Procedure Upon entering the laboratory, the task was explained to the participants, and after any questions were answered, the participants completed the informed consent and handedness forms. Retro reflective markers were placed on the appropriate anatomical landmarks, arm length and hip height were measured, and the apparatus was adjusted. A stripe of tape was placed on the floor (at a distance of 75 % of participant's arm length from the face of the drawer) and served to mark where the participants should stand during the experiment.

At the start of the trial, participants stood slightly to the left of the drawer midpoint, with the right arm by the side of the body, so that the right shoulder was aligned with the center of the drawer knob (see Figure 4.1A). At the start of each trial the experimenter verbally instructed the target mark that the object should be placed to (e.g. "blue"). The participants then opened the drawer by the knob (see Figure 4.1B), grasped the object from inside the drawer (see Figure 4.1C), and placed it on the target board in the instructed target orientation (up, left, or down, requiring 0°, 90°, or 180° object rotation, see Figure 4.1D). The participants then placed the arm back to the side of the body, and waited for the next trial to begin. Participants were instructed that all fingers should contact the objects during manipulation. Furthermore, participants were informed that accuracy was of utmost importance, and that they should move at a comfortable speed.

Each target orientation was repeated 12 times in a randomized order, yielding a total of 36 trials. The experimental session, including informed consent took approximately 20 minutes.

Data analysis The 3D coordinates of the retro reflective markers were reconstructed and labeled in VICON Nexus 1.4. Marker loss was minimal and interpolated using the gap fill procedure. The trajectories were low-pass filtered at a 5 Hz cut-off, using a second order Butterworth filter. Calculations based on the kinematic data were conducted via custom written MATLAB scripts (R2008a, The MathWorks). Prior to kinematic analysis, the wrist joint center (WJC) and the elbow joint center (EJC) were calculated as the midpoint between WRT and WRP and as the midpoint between ELL and ELM, respectively. The shoulder joint center (SJC) was calculated as 50 mm below ACR. In addition, two direction vectors were calculated, one pointing distally from the WJC to MCP (V1 = MCP-WJC), and a second one passing through the wrist (V2 = WRP - WRT). The hand center (HC) was defined on a plane normal to V1 $\times$ (V2 $\times$ V1), positioned palmar from MCP at a distance of (hand thickness + marker diameter)/2 in a way that (HC - WJC) and (HC - MCP) formed a right angle. The dependent variable of major interest was the hand orientation at each movement segment. Hand orientation was calculated as the angle (α) of the projection of the vector pointing distally from the WJC to the HC on the drawer face plane (for the initial movement segment) and on the drawer floor/ target board plane (for the intermediate and final movement segment). Hand orientations with the fingers pointing up (12 o'clock position), left (9 o'clock position), right (3 o'clock position), and down (6 o'clock position) are defined as hand orientation angles 0°, 90°, -90°, and 180°, respectively (Figure 4.2).

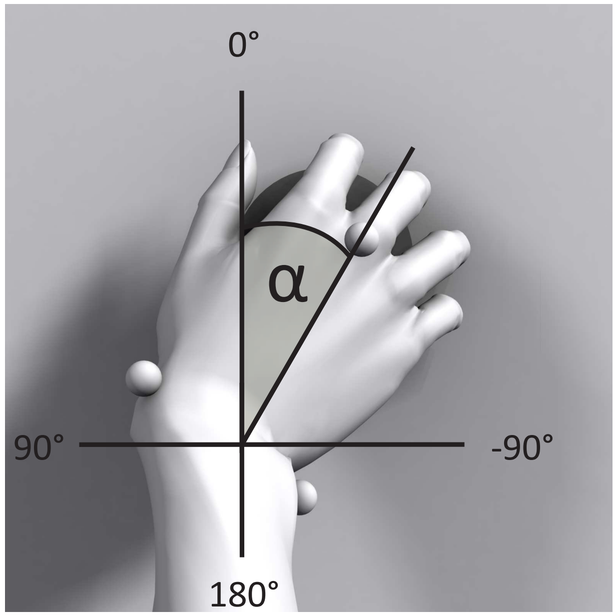

Figure 4.2: Calculation of hand orientation angle α.

Recent research (Studenka, Seegelke, Schütz, & Schack, 2012) has shown that anticipatory adjustments during sequential tasks cannot only be observed at the end effector (i.e., the hand) but also at more proximal joints of the arm. Thus, in addition to hand orientation, we also calculated the configuration of the whole arm (i.e., the seven joint angles from the shoulder, elbow, and wrist). Based on the ISB recommendations on the definitions of joint coordinate systems for the upper body (Wu et al., 2005) four body segments were defined. Thorax coordinates were defined differently from Wu and colleagues in a way that the x-axis of all segments was pointing from the back to the front of the body, the y-axis from the finger tips to the shoulder, and the z-axis pointing upwards, when participants assumed a zero position with the arm stretched towards the side and the thumb pointing upwards. Joint angles were calculated via Euler rotations between adjacent body segments. Euler rotations of the thorax to the upper arm yielded shoulder flexion/ extension, shoulder horizontal flexion/ extension, and shoulder internal/ external rotation. Euler rotations of the upper arm to the lower arm yielded elbow flexion/ extension and pronation/ supination. Euler rotations of the lower arm to the hand yielded wrist flexion/ extension and wrist abduction/ adduction.

For each trial, the time series was divided into the three movement segments: 1) drawer opening (initial movement segment), 2) object grasping (intermediate movement segment), and 3) object placing (final movement segment). The initial movement segment (drawer opening) was defined as the time period between when the hand (WJC) left the body to the time the hand grasped the drawer knob. The intermediate movement segment (object grasping) was defined as the time period between when the hand left the drawer knob to the time the object was grasped. The final movement segment (object placing) was defined as the time period between when the object was lifted from the drawer to the time the object was placed to the target board. Movement onset of each segment was determined as the time of the sample in which the resultant velocity of the hand exceeded 5 % of peak velocity of the corresponding segment. Movement offset was determined as the time of the sample in which the resultant velocity dropped and stayed below 5 % of peak velocity of the corresponding phase. Initial movement time, intermediate movement time, and final movement time was defined as the time period between movement onset and offset of the corresponding segment. Initial, intermediate, and final hand orientation and joint angles values were extracted at movement offset of the corresponding segment.

Statistical analysis analysis Hand orientation angle was analyzed using repeated measures ANOVAs with the factor target orientation [up (0° object rotation), left (90° object rotation), down (180° object rotation)][3] at the end of each movement segment (opening the drawer, grasping the object, placing the object on the target board). Movement

[3]The 0° rotation (up) condition was used as a baseline measure of grasp behavior.

times and object placement error was analyzed using repeated measures ANOVAs with the factor target orientation (up, left, down). Joint angles were analyzed using repeated measures MANOVAs with the factor target orientation (up, left, down) and the seven joint angles at the end of each movement segment as dependent variables.

Mauchly's test of sphericity was applied to test that the variance-covariance matrix of the transformed variables had covariances of 0 and equal variances. In the event that the sphericity assumption was violated the Greenhouse-Geisser correction was applied and the associated p values are reported. All significant effects were examined using Bonferroni corrected post-hoc analysis. Values are presented as means $\pm$ SE.

4.3.2 Assessment of grasp comfort

To quantify comfortable grasp postures, we obtained an independent measure of grasp comfort at the end each movement segment (i.e., drawer opening, object grasping, object placing) using a separate pool of participants (n = 14, *M* age = 26.36, *SD* = 2.37, 4 men and 10 women). Participants reported normal or corrected to normal vision, and did not have any neurological or neuromuscular disorders. The experiments were conducted in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

The experimental set up and motion capture analysis was identical to that used in the main experiment. At the start of each trial, the movement segment was specified verbally by the experimenter, and participants were told to reach out with their right hand and grasp the object with the most comfortable grasp posture. Following each response, the participant placed their hand back to the side of the body and waited for the next trial to begin. The participant performed 5 comfortable grasps in each movement segment, yielding a total of 15 trials. The entire session lasted approximately 10 minutes. The grasp postures of the comfort group were analyzed and compared to the grasp postures adopted in the grasping task.

4.4 Results

4.4.1 Object placement error

In general, object placement error was very low (mean = 4.13°) and did not differ between the 0° (3.84° ± 0.31), 90° (3.42° ± 0.52), and 180° (5.14° ± 1.16) object rotation conditions, $F(2,36) = 1.44$, $p = 0.251$.

4.4.2 Movement time

Analysis revealed that there was no effect of target orientation on initial movement time, $F(2,36) = 0.236$, $p = 0.742$. In contrast, intermediate movement time and final movement time increased with the required degree of object rotation, $F(2,36) = 34.905$, $p < 0.001$ and $F(2,36) = 15.875$, $p < 0.001$, respectively (Table 4.1). For both the intermediate and the final movement segment, post hoc tests indicated that all conditions differed significantly from each other (all $p < 0.05$).

Table 4.1: Mean movement times in ms (standard errors) as a function of target orientation

	Initial movement time	**Intermediate movement time**	**Final movement time**
Target Orientation			
0°	751(33)	1936(77)	1659(79)
90°	753(30)	2006(84)	1768(104)
180°	757(29)	2149(106)	1946(128)

4.4.3 Hand orientation

As with movement times, hand orientation angles were similar regardless of target orientation when opening the drawer, $F(2,36) = 1.90$, $p = 0.165$. The finding indicates that the final action goal did not influence grasp choice during the initial movement segment (Figure 4.3A).

In contrast, hand orientation angles when grasping the object from inside the drawer (intermediate movement segment) were influenced by target orientation [$F(2,36) = 13.16$, $p = 0.002$], indicating that participants changed their intermediate grasp posture depending on the required object end orientation. During movements to the 0° rotation target (up), participants grasped the object so that the middle finger pointed toward the 12 o'clock position (-2.69 ± 2.51°). Post-hoc analysis revealed significant differences between the hand orientation angles for 90° (left) target orientation (-12.13 ± 2.13°, 1 o'clock) compared to the 0° (up) target orientation ($p < 0.001$), and compared to the 180° (down) target orientation (23.03 ± 8.59, 11 o'clock, $p = 0.002$) indicating that the object was grasped with the hand in a more adducted (i.e., with the wrist bent toward the pinkie side) hand orientation for the 90° (left) target orientation condition than for the 0° (up) and 180° (down) orientation condition. Hand orientation angles were also significantly different for the 0° (up) orientation condition than for the 180° (down) target orientation conditions. Specifically, the object was grasped with the hand in a more abducted (i.e., with the wrist bent toward the thumb side) hand orientation for the 180° (down) target orientation compared to the 0° (up) target orientation 0° ($p = 0.022$) (Figure 4.3B).

As in the intermediate movement segment, there was an effect of target orientation on hand orientation angles at the end of the final movement segment, $F(2,36) = 6.96$, $p = 0.015$. Post-hoc analysis indicated that the object was placed with the hand in a more abducted (i.e., with the wrist bent toward the thumb side) orientation for the 90° (left) condition (-2.11 ± 2.81°) compared to the 0° (up) condition (-27.99 ± 2.85°, $p < 0.001$).

No other comparisons were significant (Figure 4.3C).

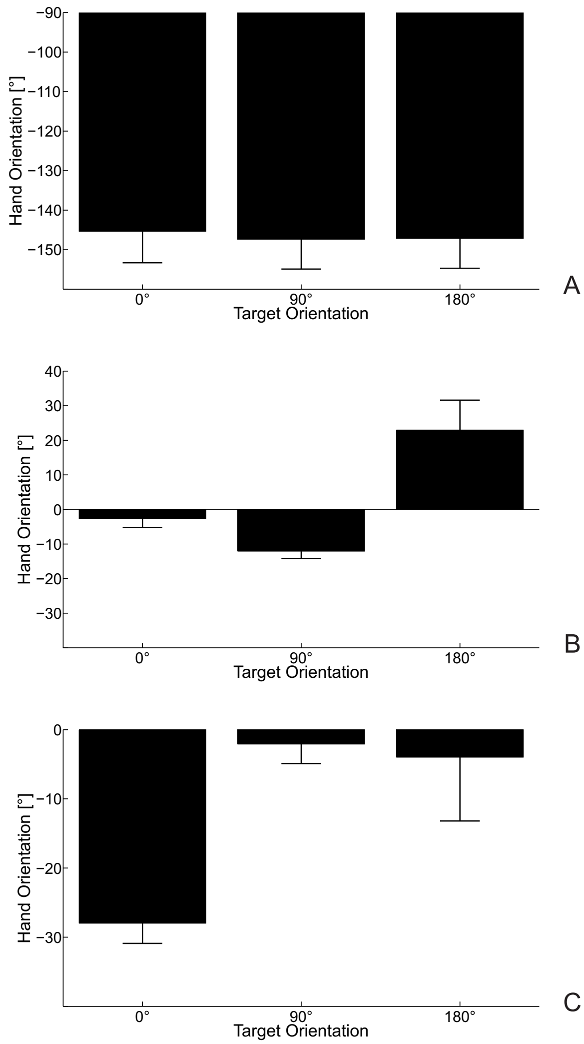

Figure 4.3: Hand orientation as a function of target orientation for A initial movement segment (drawer opening), B intermediate movement segment (object grasping), C final movement segment (object placing).

4.4.4 Joint angles

Separate repeated measures MANOVAs on the seven joint angles revealed that final target orientation did not influence the joint angles when opening the drawer, $F(14,60) = 1.55$, $p = 0.12$. Final target orientation did, however, influence the joint angles when grasping the object and when placing the object on the target [$F(14,60) = 9.84$, $p < 0.001$ and $F(14,60) = 18.93$, $p < 0.001$, respectively]. To assess which joint angles contributed to the effects, separate repeated measures ANOVAs were conducted on each joint angle at the end of the intermediate and final movement segment.

Analyses revealed that for both the intermediate and the final movement segment, all joint angles but the pronation/ supination angle were influenced by the target orientation (all $p < 0.05$, Table 4.2). As with hand orientation angles, the results on joint angles indicate that the requirements of the final task (i.e., placing the object in a certain target orientation) influenced the intermediate (grasping the object) and final movement segments (placing the object), but not the initial movement segment (opening the drawer). Given that the results obtained from the joint angle data were similar to the hand orientation angle data, the following analyses was restricted to the hand orientation angles.

Table 4.2: Mean (SE) joint angle values [°] for the different target orientation and F-values of the separate ANOVAs

Intermediate movement segment				
Joint angle		Target orientation		F
Wrist	0°	90°	180°	
Flexion/ extension	7.5(1.1)	10.4(1.1)	4.7(2.2)	4.48*
Radial/ ulnar deviation	23.7(1.4)	28.5(1.1)	9.6(4.6)	15.01**
Elbow				
Flexion/ extension	66.7(1.8)	60.5(2.5)	61.8(3.0)	4.07*
Pronation/ supination	145.0(1.8)	148.8(2.7)	148.8(2.7)	1.58
Shoulder				
Flexion/ extension	79.3(1.6)	79.3(1.6)	61.5(5.3)	14.48**
Horizontal flexion/ extension	23.6(1.5)	25.5(1.7)	33.7(2.0)	49.58***
Internal/ external rotation	23.3(1.4)	22.4(1.5)	36.5(2.3)	29.05***
Final movement segment				
Joint angle		Target orientation		F
Wrist	0°	90°	180°	
Flexion/ extension	8.5(1.1)	2.1(2.0)	-10.9(5.0)	10.02**
Radial/ ulnar deviation	4.2(1.4)	-9.8(1.0)	5.0 (3.7)	11.34**
Elbow				
Flexion/ extension	65.8(2.3)	61.2(2.5)	56.4(2.6)	29.25***
Pronation/ supination	135.3(1.4)	138.1(2.0)	143.4(4.4)	1.96
Shoulder				
Flexion/ extension	51.2(1.7)	33.7(1.8)	36.0(3.1)	19.70***
Horizontal flexion/ extension	3.7(1.3)	8.4(1.3)	12.4(1.4)	25.77***
Internal/ external rotation	-5.2(2.6)	19.4(3.2)	25.1(4.7)	24.39***

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

An unexpected result to emerge from the current experiment was the presence of individual differences in the direction of object rotation for the 180° (down) target orientation condition. 11 of the 19 participants predominantly rotated the object clockwise (in 81.8 % of the trials), whereas 8 or the 19 participants rotated the object counterclockwise (in 96.9 % of the trials)[4].

Given these individual differences, we examined whether the direction of object rotation for the 180° target orientation condition influenced the adopted hand orientation angles. Participants were separated into two groups (Clockwise Turner [CWT]) and Counterclockwise Turner [CCWT]), and only the trials in which the object was rotated according to group classification were included in the analysis. Differences in hand orientation angle at the end of the initial, intermediate, and final movement segment were assessed using separate mixed effect ANOVAs on the factors (group: CWT, CCWT) and (target orientation: up, left, down). Differences in object placement error were examined using a 2 group (CWT, CCWT) × 3 target orientation (0°, 90°, 180°) mixed effects ANOVA. Separate independent t-tests were conducted to compare differences between the two groups at each target orientation.

Analyses indicated that initial hand orientation angles were not influenced by target orientation [$F(2,34) = 2.25$, $p = 0.121$] or group, $F(1,17) = 0.016$, $p = 0.902$. The target orientation × group interaction was also not significant, $F(2,34) = 1.51$, $p = 0.235$ (Figure 4.4A).

There were significant differences in intermediate grasp postures between target orientation [$F(2,34) = 88.05$, $p < 0.001$], and group, $F(1,17) = 86.72$, $p < 0.001$. Additionally, the target orientation × group interaction was significant, $F(2,34) = 139.70$, $p < 0.001$. Post hoc t-tests revealed no differences in intermediate grasp postures between the groups

[4]Inspection of the data revealed that if the direction of object rotation differed from their typical strategy (e.g., rotating the object counterclockwise, when they typically rotated the object clockwise), this usually occurred in the first two trials. There were no observable differences in consistency between participants.

for target orientation 0° (up) [CWT = -0.61 ± 3.30°, CCWT = -5.56 ± 3.87°, p = 0.345] and 90° (left) [CWT = -11.57 ± 2.88°, CCWT = -12.88 ± 3.38°, p = 0.771]. In contrast, for target orientation 180° (down), intermediate grasp postures of the CWT were oriented more counterclockwise (63.59 ± 2.43°, 10 o'clock) compared to the CCWT [-18.33 ± 2.84°, $p < 0.001$, Figure 4.4B].

The same pattern of results emerged for final grasp postures. Analysis revealed significant differences dependent on target orientation [$F(2,34) = 59.25$, $p < 0.001$, and dependent on group, $F(2,34) = 43.87$, $p < 0.001$. The target orientation × group interaction was also significant, $F(2,34) = 176.83$, $p < 0.001$. Post hoc t-tests indicated that final grasp postures did not differ between groups for target orientation 0° (up) [CWT: -27.59 ± 3.86°, CCWT: -28.52 ± 4.52°, p = 0.877] and 90° (left) [CWT: -2.87 ± 3.78°, CCWT: -1.09 ± 4.43°, p = 0.763]. In contrast, for target orientation 180° (down), grasp postures of the CWT were oriented more clockwise (-47.15 ± 3.39°) compared to the CCWT (44.75 ± 3.98°, $p < 0.001$ (Figure 4.4C).

Object placement error was not influenced by group [$F(1,17) = 0.52$, p = 0.480], nor did the target orientation × group interaction reach significance, $F(2,34) = 2.36$, p = 0.110.

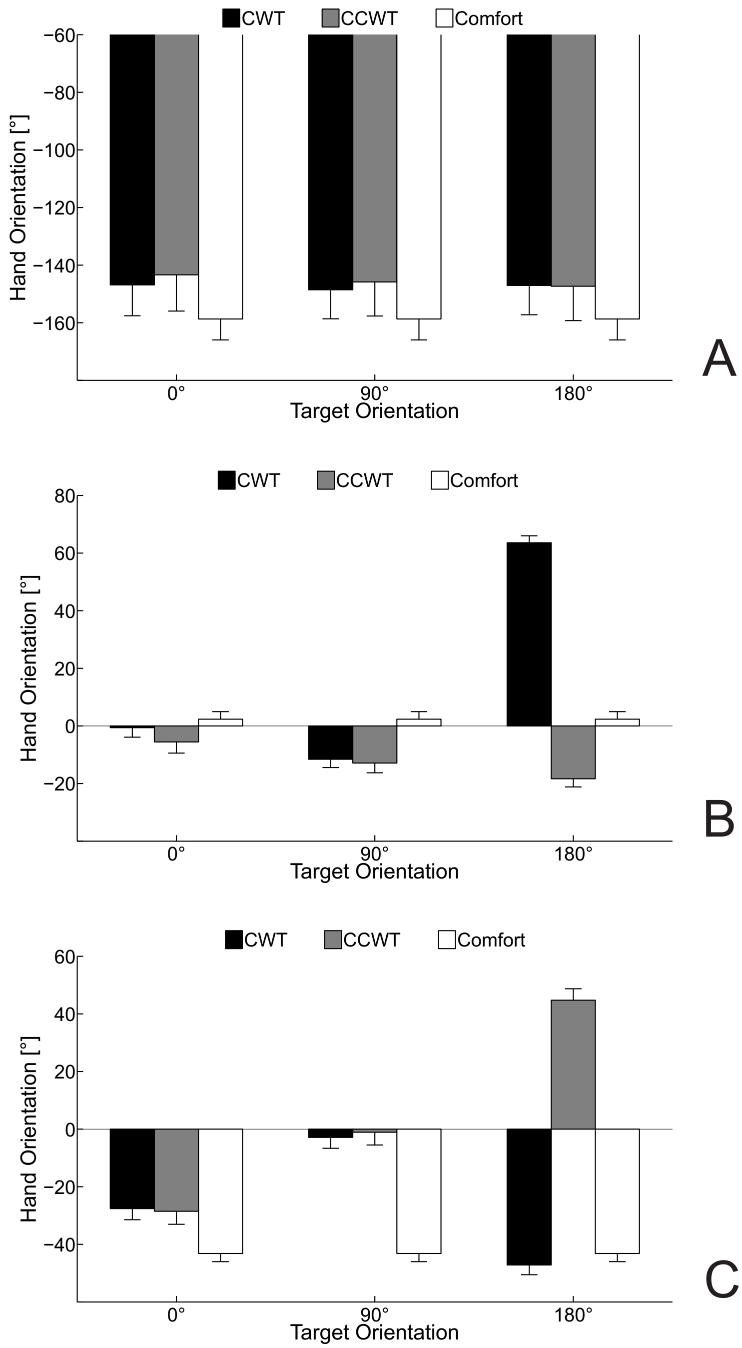

Figure 4.4: Hand orientation as a function of target orientation for A initial movement segment (drawer opening), B intermediate movement segment (object grasping), C final movement segment (object placing). Black bars indicate hand orientation of clockwise turner (CWT), gray bars of counterclockwise turner (CCWT), and white bars of the Comfort group (comfort).

4.4.5 Grasp comfort

Analysis of grasp comfort (Comfort group) indicated that hand orientation angles of -158.69 ± 7.26° were considered as most comfortable during the initial movement segment (drawer opening). Hand orientation angles of 2.35 ± 2.61° (12 o' clock hand position) were considered as most comfortable during the intermediate movement segment (object grasping). Hand orientation angles of -43.17 ± 2.83° (2 o' clock hand position) were considered as most comfortable during the final movement segment (object placing).

In the current experiment we were specifically interested in whether grasp postures are planned to optimize comfort at the end of the movement. To this end, we compared the hand orientation angles of the CWT and CCWT groups with the hand orientation angles obtained in the assessment of grasp comfort (Comfort) at each movement segment[5]. During the initial movement segment, hand orientation angles of CWT and CCWT were similar to the hand orientation angles of the Comfort group for all target orientations (Figure 4.4A).

For the 0° target orientation, intermediate hand orientation angles were also similar for all groups, indicating that participants adopted comfortable intermediate postures for this condition. Final hand orientations angles of CWT and CCWT differed slightly from the Comfort group (mean deviation: CWT = 15.61°, CCWT = 14.68°, Figure 4.4B and 4.4C). Intermediate hand orientation angles of CWT and CCWR during the 90° target orientation, deviated from intermediate hand orientation angles of the Comfort group by 13.97° for CWT, and by 15.28° for CCWT. Final hand orientation angles between CWT and the Comfort group differed by 40.33° and between CCWT and the Comfort group by 42.11° (Figure 4.4B and 4.4C). Thus, for the 90° target orientation, adopted grasp postures did neither strictly optimize comfort at the intermediate nor at the final movement segment.

[5] Because the assessment of comfortable hand orientation angles differed considerably from the assessment of grasp postures during the main experiment (i.e., different sample population, task, and instructions), the data are compared qualitatively, rather than quantitatively.

For the 180° target orientation, intermediate hand orientation angles of both CWT and CCWT were different from the Comfort group. However, the magnitude of deviation was larger for CWT (61.19°) compared to the CCWT group (20.73°). Final hand orientation angles differed considerably between the CCWT and the Comfort group (mean deviation = 87.92°). In contrast, final hand orientations of CWT were very similar to the comfortable final hand orientation angles (mean deviation = 3.98°, Figure 4.4B and 4.4C). In sum, for the 180° target orientation, the data indicates that participants who rotated the object clockwise (CWT) prioritized end-state comfort whereas participants who rotated the object counterclockwise (CCWT) prioritized intermediate comfort over end-state comfort.

4.5 Discussion

The aim of the present study was to investigate anticipatory planning during a multi-segment object manipulation task. Based on previous literature (Haggard, 1998; Hesse & Deubel, 2010a) we hypothesized that grasp postures during both the intermediate (i.e., when grasping the object from the drawer) and initial movement segment (i.e., when grasping the drawer) would be influenced by the final action goal of the task (i.e., specific end orientation when placing the object on the target). Our findings, however, do not support this prediction. We found that the movement end-goal influenced grasp postures during the intermediate, but not the initial movement segment, indicating that participants did not plan the entire movement sequence holistically in advance.

Although there is a possibility that anticipatory planning is limited to a single object, the finding that motor planning extends to tasks in which multiple objects are manipulated (Hesse & Deubel, 2010a, Experiment 1), indicates that such an explanation is unlikely. We hypothesize that the ability to plan for the entire movement was influenced by the degree of precision required during the final movement segment (see also Alberts, Saling, & Stelmach, 2002; Haggard & Wing, 1998; Hesse & Deubel, 2010a, 2010b; Rand

& Stelmach, 2000). For example, in Hesse and Deubel (2010a, Experiment 2) participants performed the same multi-segment movement sequence described in the introduction Hesse and Deubel (2010a, Experiment 1), except that the precision demands of the second movement segment (i.e., placing the cylinder) were increased. Instead of placing the cylinder on a target circle, participants had to place the first object on a pin located in the center of the target circle. Hesse and Deubel found that the increased precision demands affected the planning process, such that the grip orientation in the early movement segments was no longer influenced by the orientation of the bar in the last movement segment. The authors argue that the higher task demands might have required more planning resources and thus prevented a holistic planning process.

The results of the current experiment support this proposition. After grasping the object from the drawer, participants had to align the black mark located on the top of the object (0.5 cm wide) with the appropriate colored mark (0.5 cm wide) located on the target board. We maintain that this action required a high level of precision at the end of the movement sequence. Thus, the high precision demands in the present task might have required vast cognitive costs associated with motor planning and programming. To mitigate these cognitive costs, participants might have adopted a sequential planning strategy. In other words, participants generated two different movement plans (one for the drawer opening and another for grasping and placing the object) to reduce the cognitive motor planning costs. One way in which this hypothesis could be tested is by reducing the precision demands at the final movement segment (e.g. double the width of the target marks). If the ability to plan in a holistic fashion is influenced by the high precision requirements, then one would expect to observe a shift from sequential to holistic performance when end point precision requirements are reduced, and the final target orientation would also influence initial grasp postures.

In this study we examined whether individuals are able to plan their grasp postures to optimize end-state comfort during a three-segment action sequence in which they can select from a continuous range of possible grasp postures. Based on the comfort ratings, intermediate hand postures were defined by orientation angles of 2.35° (12 o'clock hand position), and comfortable final postures were defined by hand orientation angles of -43.17° (2 o'clock hand position). Comparison of the object manipulation task with the comfort ratings data indicated that participants selected a comfortable grasp posture (-2.69°, 12 o' clock hand position) when grasping the object from inside the drawer for the 0° target orientation condition. This grasp posture resulted in a final grasp posture (-27.99°, 1 o'clock position) that was slightly different from a comfortable final posture (mean deviation = 15.18°). In contrast, participants typically grasped the object from the drawer with an average hand orientation angle of -12.13° (1 o'clock position) for the 90° (left) target orientation condition, which resulted in average final hand orientation angles of -2.11° (12 o'clock position). Thus, comparing the hand orientation angles for the 90° rotation (left) and the 0° rotation (up) condition, intermediate grasp postures were less comfortable for the 90° rotation condition, indicating that participants sacrificed comfort when grasping the object from the drawer so that the hand could be placed in a more comfortable posture at the end of the movement. However, the deviation from comfortable hand orientation angles at the end of the movement (when placing the object on the target board) was larger for the 90° rotation condition (41.06°) compared to the 0° rotation condition (15.18°) suggesting that postures are not planned to strictly optimize end-state comfort.

At first glance the results of the current experiment are incongruent with the corpus of work demonstrating that end-state comfort is a primary motor planning constraint (e.g., Rosenbaum et al., 1990; Rosenbaum, Vaughan, Barnes, & Stewart, 1993; Short & Cauraugh, 1999; Weigelt, Kunde, & Prinz, 2006). However, the critical difference between previous research and the present study is that previous studies limited the range of possible hand orientations that could be adopted. In the aforementioned studies, participants had to choose between two distinct grasp postures (i.e., overhand vs. underhand grasp).

A limitation of these dichotomous grip choice tasks is that they do not allow for moderate comfort at both the start and the end of the movement, instead forcing participants to sacrifice comfort at the start of the movement if they wish to satisfy end-state comfort. More recent studies in which an object is to be rotated have indicated that the sensitivity toward comfortable end-states differs in tasks where participants can select from a continuous range of possible grasp postures (e.g., Herbort & Butz, 2010, 2012). For example, Herbort and Butz (2010) asked participants to grasp a circular knob and rotate it 45°, 90°, or 135° in a clockwise or counterclockwise direction. They found that participants selected initial grasp postures to afford end-state comfort, but that, the extent of end-state comfort sensitivity was strongly influenced by the direction of rotation, as well as the degree of object rotation. Thus, evidence from the present study as well as the studies of Herbort and Butz (2010, 2012) suggests that individuals plan their movements to afford moderately comfortable grasp postures at the intermediate and final movement segments, rather than for end-state comfort alone. Compared to grasp postures that optimize comfort at the end of the movement (which necessitate that participants sacrifice comfort at the start of the movement), this 'weighted comfort'strategy negates extremely awkward and uncomfortable positions at discrete points in time (e.g., when placing the object on the target board). The results of the present study do not provide information about the precise distribution of the "weighted comfort" between the intermediate and final movement segments. It is possible that individuals distribute comfort between the two time periods equally. Conversely, the possibility exists that individuals weight comfort higher at one time point than at the other time point.

An interesting finding to emerge from the present study was the presence of individual differences for movements that required 180° rotation. We found that some participants preferred to rotate the object counterclockwise (n = 8), while others preferred to rotate the object clockwise (n = 11). Participants who preferred counterclockwise rotations typically grasped the object from the drawer with the hand in a 1 o'clock orientation

(-18.33°), which resulted in final grasp postures (44.75°, 10 o'clock) that were considerably different from what was expected based on the comfort ratings data (-43.17°, 2 o'clock). In contrast, participants who rotated the object clockwise typically grasped the object from the drawer with the hand in a 10 o'clock orientation (63.59°), which resulted in final grasp postures (-47.15°, 2 o'clock) that were similar to the comfortable final postures. Thus, the data indicate that participants who preferred counterclockwise rotations prioritized comfort at the intermediate grasp over end-state comfort while participants who preferred clockwise rotations weighted end-state comfort higher than comfort at the intermediate grasp.

Individual differences in selection of movement strategies have been reported before during unimanual (Hughes, Seegelke, & Schack, 2012; Rosenbaum, van Heugten, & Caldwell, 1996) and bimanual synchronous movements (Fischman, Stodden, & Lehmann, 2003; Hughes & Franz, 2008; Hughes, Seegelke, Reißig, & Schütz, 2012; Janssen, Crajé, Weigelt, & Steenbergen, 2010). For example, in the study of Janssen et al. (2010) participants grasped two bars and placed them in target boxes with either the left end or the right end pointing down. Although the majority of participants adjusted their initial grips so that they could end the movement in a comfortable posture (i.e., thumb-up posture), there was a subset of participants who always grasped the bars with the same initial grips, irrespective of the required end-orientation of the bars. The authors argue that the latter group weighted comfort at the start posture higher than end-state comfort and suggest that these participants might be "less proficient planners" (Janssen et al., 2010, p. 251).

Although it is certainly plausible that these participants were less efficient planners than the participants who planned for end-state comfort, we have an alternative explanation for these differences. In the present task, the instructions of the task emphasized accuracy, and participants were not only able to satisfy the action goals of the task, but were highly accurate in doing so. Thus, we postulate that some individuals prioritized comfortable start postures or averaged comfort, which in our opinion does not necessarily imply that these individuals have compromised motor planning abilities. The results of the current experiment do not allow us to determine whether this subset of participants prioritize start or averaged comfort, or have compromised planning abilities. One possible solution to dissociate between these two explanations would be to examine motor planning across a number of different tasks. If the participants in the present task who did not behave in accordance with end-state comfort are less proficient planners, they should also exhibit poor planning abilities across a range of tasks. In contrast, if these participants prioritize comfort at different stages in the action sequence, then we would expect that they would exhibit likewise behavior in similar tasks (i.e., prioritizing intermediate-state comfort), but that planning performance in other tasks would be comparable to the general population.

In sum, the results of the present study build on previous research from our laboratory (Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; Hughes, Seegelke, Reißig, & Schütz, 2012; Hughes, Seegelke, & Schack, 2012; Seegelke, Hughes, & Schack, 2011) in which we advocate the perspective that movements are first planned with respect to the action goals of the task. These action goals, in turn, serve to guide lower-level constraints, such as grasp posture planning. The process and selection of appropriate grasp postures is influenced by not only the task, but by the internal state of the individual. Specifically, each individual optimizes their own performance by selecting lower-level constraints that allow for successful completion of the action goal, and the selection of these constraints is dependent upon contextual, environmental, and internal influences. The chosen constraints are then weighted relative to one another, forming a task-specific constraint hierarchy. As our results suggest, individual differences in task conceptualization and optimization lead some participants to prioritize end-state comfort, and other participants to prioritize comfort at the intermediate, rather than at the final, movement segment.

Author contributions

Conceived and designed the experiments: CSee, TS. Performed the experiments: CSee. Analyzed the data: CSee. Contributed reagents/ materials/ analysis tools: CSee, CSch. Wrote the manuscript: CS, CMLH.

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5 General Discussion

Anticipatory grasp posture planning has been extensively studied during object manipulation tasks composed of two action segments (second-order planning, see Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012, for a review). Initial studies in which participants grasped a bar from a home position and placed it to a target position (e.g., Rosenbaum et al., 1990) demonstrated that participants selected initial grasp postures depending on which end of the bar was to be brought to the target. Namely, initial grasps were chosen such that they always ended the movement in a comfortable or easy-to-control posture. Since its original description, the end-state comfort effect has been reproduced in number of subsequent studies, and appears to be a dominant action selection constraint during unimanual object manipulation tasks (e.g., Hughes, Seegelke, Spiegel, et al., 2012; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992; Rosenbaum, Vaughan, Barnes, & Stewart, 1993; Short & Cauraugh, 1997, 1999). More generally, the end-state comfort has been taken to support the notion that people mentally represent future body states and select initial grasp postures in anticipation of these forthcoming postures.

More recently, research has elucidated additional factors that are considered during grasp posture planning which that interact with the tendency toward end-state comfort. For example, a decreased sensitivity towards end-state comfort has been observed when the bar-transport task involves 180° as opposed to 90° object rotation (i.e., moving the bar from a vertical start position to a vertical target position, e.g., Hughes & Franz, 2008; Hughes, Seegelke, & Schack, 2012; Seegelke, Hughes, & Schack, 2011). Similarly, employing continuous instead of binary measures of grasp selection has provided evidence that grasp posture planning is influenced by the required direction and degree of rotation (e.g., Herbort & Butz, 2010, 2012). In addition, other action selection constraints such as sequential effects (R. G. Cohen & Rosenbaum, 2004, 2011; Rosenbaum & Jorgensen, 1992; Schütz & Schack, 2013; Schütz, Weigelt, Oderken, Klein-Soetebier, & Schack, 2011), dominant hand bias (Coelho, Studenka, & Rosenbaum, in press), object affordances (Sartori, Straulino, Castiello, & Avenanti, 2011), or habitual factors (Herbort

& Butz, 2011) have been shown to interact with end-state or goal-oriented grasp selection criteria indicating that the end-state comfort effects is not as pronounced as has been reported during the bar-transport paradigm. In sum, although there is a large corpus of research that have examined action selection constraints on grasp postures planning during two-segment object manipulation tasks, surprisingly little work has considered action selection constraints during multi-segment object manipulation tasks (Haggard, 1998; Hesse & Deubel, 2010; Rosenbaum et al., 1990).

The research presented in the current thesis examined action selection constraints during grasp posture planning. Specifically, it focused on the following constraints during multi-segment object manipulation tasks – (1) the tendency to select initial grasp postures that allow for control or comfort at later stages, (2), the tendency to minimize postural transitions between immediately forthcoming and subsequent postures, and (3) the tendency to consider early action segments more thoroughly as compared to later segments (i.e., planning gradient), as well as potential interactions between these constraints.

5.1 Interaction of biomechanical and cognitive factors

Chapter 2 assessed to what extent biomechanical and cognitive factors contribute to grasp posture planning during multi-segment object manipulation tasks, and whether participants would adjust their initial grasp postures over time. To this end, participants performed a grasping and placing task consisting of one, two, or three movement segments. The position of the targets was manipulated such that the degree of required object orientation between the home and the first target positions, and between the first and the second target positions, varied. Complementing previous work (e.g., Christina, 1992; Fischman, 1984; Henry & Rogers, 1960; Klapp, 1995, 2010; Sternberg, Monsell, Knoll, & Wright, 1978), the time to plan the manual action increased with the number of segments in the sequence and with the required degree of object rotation. In addition, participants selected initial grasp postures that were inversely related to both the first and second target positions, suggesting that the multi-segment action sequences were planned holistically in advance, and that each element was considered during grasp posture planning. These findings are consistent with other studies employing a continuous grasp posture measure (R. G. Cohen & Rosenbaum, 2004; Herbort & Butz, 2010, 2012; Seegelke, Hughes, & Schack, 2013; Zhang & Rosenbaum, 2008) that also reported inverse relationships between initial grasp posture selection and target position, and have suggested that participants planned the sequence such that they adopted postures that allowed for comfort or control at later stages in the sequence. The first study that examined grasp posture planning during a three-segment movement sequence (Rosenbaum et al., 1990) has indicated that participants would plan for intermediate- rather than end-state comfort. However, a potential drawback of this study was that the task required participants to select from either one of two grasps (overhand vs. underhand). Consequently, in the critical conditions, participants could only satisfy intermediate- or end-state comfort, but could not distribute comfort between these two positions. The results presented in Chapter 2 indicate that if participants can select from a continuous range of postures they will not satisfy comfort or control at a single target position but rather seek to adopt postures that are (within limits) controllable at both target positions. Such an interpretation is also congruent with recent studies examining grasp posture planning during two-segment action sequences (Herbort & Butz, 2010, 2012) which reported that end-state comfort is not strictly optimized but that grasp posture planning is sensitive to the direction and extent of required object rotation.

Interestingly, the results presented in Chapter 2 further revealed that initial grasp postures were differently adjusted to the target positions depending on the temporal order in which the object was to be placed to these targets. On average, the first target position exhibited a stronger influence on initial grasp posture selection compared to the second target position. Such a finding supports the existence of a planning gradient (i.e., a cognitive action selection constraint), which states that action segments that occur temporally earlier in an action sequence are considered to stronger degree in an action plan as compared to segments that occur later. Evidence for a planning gradient in motor planning has been reported in other studies (e.g., Haggard, 1998; Land, Rosenbaum, Seegelke, & Schack, 2013) and might also explain the results of Rosenbaum et al. (1990). More generally, a gradient of advance motor planning is reminiscent of the digit span or serial position effects typically observed in memory tasks (see Conway et al., 2005, for a review). Consequently, it might be speculated that working memory plays a crucial role in motor planning. Support for this hypothesis was obtained in recent studies that reported interference between motor planning and concurrent working memory performance (Logan, Miller, & Strayer, 2011; Spiegel, Koester, & Schack, 2013a, 2013b; Spiegel, Koester, Weigelt, & Schack, 2012; Weigelt, Rosenbaum, Huelshorst, & Schack, 2009) indicating that motor planning and working memory share common cognitive resources.

As reported in Chapter 2, the stronger influence of the first target position compared to the second target position on initial grasp posture was particularly pronounced during the initial stages of the experimental session. However, after several trials the influence of the second target position increased, especially when the range of optimal control at this position was considered to be small. These findings suggest that participants could overcome the cognitive limitations in advance planning (i.e., a planning gradient) by adjusting their initial grasp postures more strongly to the requirements of the second target positions.

Together, these findings demonstrate that the planning of initial grasp postures is influenced by both biomechanical and cognitive factors. Moreover, the adaptations in initial grasp postures indicate that the relative influence of these constraints is not fixed but rather flexible. The notion of a flexible constraint hierarchy has been appreciated before in the context of bimanual object manipulation (e.g., Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; van der Wel & Rosenbaum, 2010).

Previous work has demonstrated that when performing bimanual movements, there is a strong tendency for the limbs to stay temporally and spatially coupled (Franz, 2003; Franz, Eliassen, Ivry, & Gazzaniga, 1996; Franz, Zelaznik, & McCabe, 1991; Franz, Zelaznik, Swinnen, & Walter, 2001; Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979; Oliveira & Ivry, 2008). In the context of grasping, this coupling is reflected in the tendency to adopt similar grasp postures. Accordingly, during bimanual object manipulation tasks typically two action selection constraints are contrasted. Participants must weigh the tendency to adopt initial grasp postures that allow for comfortable end-postures against the tendency to adopt identical grasps. Previous research has demonstrated that participants will satisfy bimanual end-state comfort rather than bimanual coupling (i.e., identical grips) when the required object end-orientation is congruent (Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; Hughes, Reißig, & Seegelke, 2011; Hughes & Seegelke, 2013; Hughes, Seegelke, & Reißig, 2014; Hughes, Seegelke, Reißig, & Schütz, 2012; Weigelt, Kunde, & Prinz, 2006, i.e., when the same degree of object rotation is required,). In contrast, when the objects were placed in incongruent end-orientations, bimanual coupling is satisfied as often as bimanual end-state comfort (Hughes & Franz, 2008; Hughes, Haddad, et al., 2011; Hughes, Reißig, & Seegelke, 2011; Hughes et al., 2014; Hughes, Seegelke, Reißig, & Schütz, 2012; Janssen, Beuting, Meulenbroek, & Steenbergen, 2009; Janssen, Meulenbroek, & Steenbergen, 2011).

Consistent with the findings presented in Chapter 2, these results suggest that constraints take on different degrees of importance depending on the nature of the task and on the level of task experience (van der Wel & Rosenbaum, 2010).

5.2 Comfort planning vs. postural transition minimization

Chapter 3 examined the interplay between the tendency to select grasp postures that allow for comfortable or easy-to-control postures at later stages and the tendency to minimize differences between immediately forthcoming and subsequent postures during a three-segment object manipulation task. The idea that actions might be selected to minimize postural transitions (Studenka, Seegelke, Schütz, & Schack, 2012), or more generally transitions through task space (Fowler, 2007; Jordan & Rosenbaum, 1989; Rosenbaum, Chapman, Coelho, Gong, & Studenka, 2013) might be an effective means to reduce the cognitive costs associated with grasp posture planning in prospective action control. That is to say, by making two (or more) consecutive grasp postures in an action sequence more similar, the central nervous might attempt to reduce the costs of changing movement plans (Hesse & Deubel, 2010; Studenka et al., 2012). Hesse and Deubel (2010) found that participants' grip orientations of preceding segments were systematically shifted towards final grip orientation reinforcing the interpretation that participants minimized postural differences. A potential critical difference of their work when compared to other studies was that the placement of the object at the first target position did not require a specific orientation. It might thus be speculated that this manipulation prompted participants to attribute a higher weight to the tendency for minimizing postural differences. To directly contrast these two action selection constraints, we adapted the experimental task described in Chapter 2 such that the object orientation at the first (intermediate) target position was unconstrained, and participants were free to place the object in any desired orientation (similar as in Hesse & Deubel, 2010). Thus, participants reached and grasped a cylindrical object from a home position, placed it at an intermediate target position in a freely chosen orientation, and subsequently placed it at one of four final target positions in a predetermined orientation.

On average, initial grasp postures were inversely related to final target orientation. In contrast, intermediate grasp postures were not influenced by final target orientation, but similar to the most comfortable postures obtained at this position. Hence, these results accord with those of Chapter 2 and previous studies (Zhang & Rosenbaum, 2008) suggesting that participants not only selected initial grasp postures that afford control at the end of the movement sequence (end-state comfort) but also at the intermediate target position (intermediate-state comfort). Thus, at first glance, the tendency to select grasp postures that allow for comfortable or easy-to-control postures at later stages seems to be weighted higher than the tendency to minimize differences between immediately forthcoming and subsequent postures.

However, closer inspection of the data revealed inter-individual differences in initial grasp posture selection, ranging from very strong to virtually no adjustment. In this task, strong adjustments in initial grasp postures led to more comfortable final grasp postures, whereas small adjustments led to less comfortable final postures. Interestingly, intermediate grasp postures were similar (and close to the most comfortable intermediate grasp postures) regardless of initial grasp posture adjustment. Consequently, it is possible that participants who strongly adjusted their initial grasp postures to the final target positions planned the action sequence such that they adopted initial grasp posture that allow for more control at later stages. In contrast, participants who selected similar initial grips regardless of final target position did not minimize postural transitions between the intermediate and final grasp postures, as intermediate grasp postures were not influenced by final target orientation. However, these participants might have aimed at minimizing postural differences between the initial and intermediate grasp postures as these were highly similar. That way, they were able to not only reduce the cognitive costs by selecting similar initial grasps, (see also Hughes, Seegelke, Reißig, & Schütz, 2012), but also to assure comfortable intermediate grasp postures.

5.3 Extension to two-object manipulation tasks

Chapter 4 examined whether participants would plan for comfort at later stages during a three-segment object manipulation tasks in which two objects are manipulated. In this task, participants opened a drawer, grasped an object from inside the drawer, and subsequently placed the object on a table in one of three different target orientations (0°, 90°, or 180° object rotation required). It was of interest to examine to what extend the final target orientation would influence grasp posture of the preceding segments, and whether grasp postures are planned to optimize end-state comfort. Results showed that initial grasp postures (i.e., when opening the drawer) were not influenced by the final target orientation, indicating that participants did not plan the entire movement sequence holistically in advance. In contrast, both the intermediate (i.e., when grasping the object) and the final grasp posture (i.e., when placing the object) were influenced by the final target orientation. Comparing intermediate and final grasp posture for the 0° and 90° target orientation condition with the most comfortable intermediate and final grasp postures revealed that participants did not strictly optimize comfort at one of these positions. Rather, these results complement those of Chapter 2 and those of previous studies (Herbort & Butz, 2010, 2012) suggesting that participants planned their movements to afford moderately comfortable postures at both the intermediate and final movement segment. For the 180° target orientation condition participants adopted different strategies (i.e., inter-individual differences) to achieve the action goal. Specifically, 42 % of the participants were able to successfully complete the action goal by adopting grasp postures that were comfortable at the intermediate but not the final position (intermediate-state comfort) and rotated the object counterclockwise. In contrast, 58 % of the participants preferred clockwise rotations and adopted grasp postures that allow for comfort at the end of the movement but not at the intermediate position (end-state comfort). These results provide further evidence that grasp posture planning is strongly influenced by the required degree of object rotation (e.g., Herbort & Butz, 2010, 2012), and indicate that participants might prioritize comfort at different stages in an action sequence, especially when larger degrees of object rotation are required (see also Seegelke et al., 2011).

5.4 Interplay of action selection constraints and inter-individual differences

To sum up, the research presented in Chapters 2, 3, and 4 have demonstrated that multiple action selection constraints are considered and interact during the planning and execution of multi-segment object manipulation tasks. Specifically, the results in Chapter 2 provide an example for the interplay between biomechanical (i.e., planning for comfort at later stages) and cognitive (i.e., planning gradient) constraints. The major findings to emerge from Chapter 3 and 4 was the presence of inter-individual differences in grasp posture selection suggesting that participants prioritized different constraints during task performance. One notable difference between Chapter 2 and 3 and Chapter 4 is that in the latter there was no evidence that participants planned the entire action sequence holistically in advance. Specifically, intermediate and final grasp postures were influenced by the final target orientation, but not initial grasp postures. As described in Chapter 4, it seems unlikely that this lack of advance planning can be attributed to the fact that two objects were to be manipulated in Chapter 4 (see Hesse & Deubel, 2010). In addition, the proposed explanation that the high precision demands alone might have prevented a holistic planning process (see also Hesse & Deubel, 2010, Experiment 2) appears not terribly satisfying, as the precision demands in Chapter 2 and Chapter 3 were not considerably lower.

Another potential explanation that can account for the observed results of this thesis was offered by Rosenbaum et al. (2012). In all studies that found evidence for planning beyond the second order (Haggard, 1998; Hesse & Deubel, 2010; Chapter 2, Chapter 3), the targets occupied a single plane, whereas in studies that failed to find evidence (Rosenbaum et al., 1990; Chapter 4) multiple planes were occupied. When an object must be brought to targets located in different planes there are more joints involved compared to when targets are located in a single plane. Consequently, it might be speculated that there are more degrees of freedom in the limb that need to be controlled, thus, increasing the cognitive costs associating with motor planning. Whether this difference can account for the results remains a challenge for future research.

In the remainder of this thesis, these findings will be discussed in view of the theoretical models of action control outlined in Chapter 1. A specific emphasis will be given to the issue of how the presence of inter-individual differences can be understood and incorporated into those models.

5.5 Constraint hierarchies

As mentioned in Chapter 1, constraints that limit the range of possible actions provide one way of how the central nervous system copes with the degrees of freedom problem (Bernstein, 1967). This applies even to apparently simple motor tasks such as grabbing a cup to drink from it. Consequently, identifying those constraints that allow for successful task performance is a major challenge for researches interested in motor control.

From a cognitive psychology perspective, it has been proposed that action selection is the process in determining a ranking or weighting of different constraints, which is guided by the action goals of the task (Hughes & Franz, 2008; Hughes, Haddad, et al., 2011; Hughes, Seegelke, & Schack, 2012; Rosenbaum et al., 2013; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; Seegelke et al., 2011; van der Wel & Rosenbaum, 2010. Although this idea might appear trivial, given that the field of motor control has largely been neglected by psychologists (Rosenbaum, 2005), the prevalent view in the engineering-inspired motor control research diverges from it. Specifically, these perspectives opine that of all possible actions that could potentially achieve a given goal, actions that are eventually selected optimize an intrinsic cost related to a single criterion. Proposed criteria include the minimization of mean squared jerk (Hogan, 1984; Hogan & Flash, 1987), minimization of torque change (Uno, Kawato, & Suzuki, 1989), and minimizing endpoint variance (Harris & Wolpert, 1998). However, movements do not always satisfy these constraints. Indeed, the variables to be optimized may vary depending on the task to be executed, thus, constraints might not always be equally important. Consequently, a beneficial component of a theoretical framework which proposes that action selection is based on constraint hierarchies it that it does not require the inclusion or exclusion of constraints, but rather includes all possible constraints. The importance of those constraints is differentiated by assigning different weights to them (Rosenbaum et al., 2013).

The ranking or weighting of constraints is assumed to be not static. Rather, constraints can be re-prioritized according to the task to be achieved. Support for the idea of flexible constraint hierarchies comes from the bimanual grasping and placing literature (Fischman, Stodden, & Lehmann, 2003; Hughes & Franz, 2008; Hughes, Haddad, et al., 2011; Hughes, Reißig, & Seegelke, 2011; Hughes et al., 2014; Hughes, Seegelke, Reißig, & Schütz, 2012; Janssen et al., 2009; Janssen, Crajé, Weigelt, & Steenbergen, 2010; Janssen et al., 2011; van der Wel & Rosenbaum, 2010; Weigelt et al., 2006. Bimanual grasping and placing provides an excellent opportunity to examine the interplay of action selection constraints as two well-known constraints can be contrasted, namely end-state comfort and bimanual symmetry (i.e., the tendency to produce similar spatio-temporal movement patterns with the two hands). For example, in the studies by Hughes and colleagues (Hughes, Haddad, et al., 2011; Hughes, Reißig, & Seegelke, 2011; Hughes et al., 2014; Hughes, Seegelke, Reißig, & Schütz, 2012), participants simultaneously reached and grasped two objects and transported them to two target locations. The authors manipulated the required end-orientations such that they were either congruent (i.e., same degree of object rotation required) or incongruent (i.e., different degree of object rotation required). For the congruent conditions, participants overwhelmingly adopted initial grasp postures that satisfied end-state comfort for both ends, even if they had to adopt different initial grasps. In contrast, for the incongruent conditions, participants did neither satisfy end-state comfort nor bimanual coupling in a reliable fashion.

Similarly, in van der Wel and Rosenbaum (2010) participants grasped and moved two plungers from the two start locations to two target locations located at either the same (i.e., both high or both low) or different target locations (i.e., one high, one low). Participants grasped the plungers symmetrically and at heights that ensured comfortable end-posture when the targets where located at the same height. However, when the targets were located at different heights, these tendencies were reduced. Moreover, when the plungers had different mass distributions, participants weighted end-state comfort higher than bimanual symmetry, with the difference in weighting increasing with repetition. These findings reinforce the assumption that different task demands (i.e., object end-orientation/ target height congruency) as well as experience (i.e., repetition) influence the relative weighting of action selection constraints, thus influencing action selection processes.

The results of Chapter 2 are certainly in line with this view as they demonstrate the interplay between biomechanical and cognitive action selection constraints. Specifically, in this task, participants selected initial grasp postures based on the specific requirements of the first and second targets, and initial grasp postures were differently adjusted depending on the temporal order in which the object was to be placed to these targets. In addition, initial grasp posture selection was influenced, to a larger extent, by the first target demands during the initial stages of the experimental session, suggesting that the cognitive constraint (i.e., planning gradient) was ranked higher in the constraint hierarchy. However, with several repetitions, participants could overcome the cognitive limitations and consequently adjusted their initial grasp postures more strongly to the requirements of the temporally distal target, thereby indicating that they re-prioritized constraints over the experimental session.

As already pointed out by van der van der Wel and Rosenbaum (2010), these results may contribute to the understanding of perceptual-motor skill learning. Skill learning is accompanied by increased sensitivity to nuances in performance, including the perceptual consequences of performance. van der Wel and Rosenbaum (2010) argue that this increased sensitivity is caused by changing the relative importance of constraints. Initially, all possible constraints are assigned weights based on similarities to other tasks. However, the relative importance of these constraints may change over time enabling better performance. How exactly the weighting of constraints change over time is a topic for future research.
This idea can also be applied to the cognitive architecture model (Schack, 2004), which hold that BACs serve as representational units for movements which tie together the functional and sensory features of movements on a level of mental representation. Similarly, a constraint hierarchy can be viewed as a specific representation structure located at this level. It has been shown that cognitive representation structures change over the course of early skill acquisition of a motor task, and that this change comes along with improved motor performance (Frank, Land, & Schack, 2013). Accordingly, perceptual-motor skill learning can be viewed as the modification and adaptation of representation structures or constraint hierarchies.

5.6 Inter-individual differences

The major finding to emerge from Chapter 3 and 4 was the presence of inter-individual differences in grasp posture adjustment during the planning of multi-segment object manipulation tasks. Specifically, in Chapter 3 notable inter-individual differences in initial grasp postures were observed ranging from very strong to virtually no adjustment. Although these differences in initial grasp postures resulted in differences in final grasp postures (i.e., stronger adjustment led to more comfortable final grasp posters), intermediate grasp postures were similar regardless of initial grasp posture adjustment. In Chapter 4, participants adopted different intermediate grasp postures when the object required 180° rotation. Specifically, in this condition 42 % of the participants adopted grasp postures that were comfortable at the intermediate position (intermediate-state comfort) but not the final position, and rotated the object counterclockwise. In contrast, 58 % of the participants preferred clockwise rotations, and adopted grasp postures that allow for comfort at the end of the movement but not at the intermediate position (end-state comfort).

The presence of inter-individual differences in grasp posture planning has been reported before during both unimanual (Hughes, Seegelke, & Schack, 2012; Rosenbaum et al., 1990; Rosenbaum, van Heugten, & Caldwell, 1996) and bimanual object manipulation tasks (Fischman et al., 2003; Hughes, Seegelke, Reißig, & Schütz, 2012; Janssen et al., 2010). Before potential explanations for the inter-individual differences of the present thesis are offered, these studies are summarized first.

The initial study that examined the influence of future task demands on initial grasp posture selection (i.e., bar-transport task) already mentioned inter-individual differences (Rosenbaum et al., 1990). Specifically, the authors reported that in one of their experiments (Experiment 2), 50 % of the participants picked up the bar and then rotated it within the hand. This strategy allowed the participants to always avoid awkward grasp postures (see also Hughes & Franz, 2008).

Similar observations were reported by (Rosenbaum et al., 1996) when exploring the precision hypothesis as a potential explanation for the end-state comfort effect. In this task, participants grasped a handle connected to a disk and turned the handle to a designated target. When the handle past the target, a bolt would drop into a whole at this location. As the task did not require precise positioning of the handle, according to the precision hypothesis the authors reasoned that participants should always select same initial grasps, hence, the end-state comfort effect should be attenuated. Although 50 % (n = 4) of participants behaved in accordance with the authors' expectations, the other 50 % switched

initial grasp postures such that they adopted comfortable postures at the target position. Remarkably similar results were recently obtained in a study that examined the influence of precision demands at the start and the end of the movement (Hughes, Seegelke, & Schack, 2012). In this task, participants reach and grasped a cylinder located in a start disk and moved it to a target disk. The size of the disks was manipulated so that the precision demands at the start and end of the movement were either identical (low initial and final precision, high initial and final precision) or different (low initial and high final precision, high initial and low final precision). The authors found that 50 % of participants generally planned their movements in way that ensured comfortable end-postures regardless of the precision requirements. In contrast, the other half of participants changed their initial grasp postures based on the precision demands of the task, and were more likely to select initial grasps that resulted in end-state comfort compliant grasp postures when the final precision demands were high than when they were low. Thus, as in Rosenbaum et al. (1996), half of the participants acted in accordance with the precision hypothesis whereas the other half satisfied end-state comfort regardless of the precision demands of the task.
Individual differences in grasp posture planning have also been found during bimanual object manipulation tasks. For example, in the study of Janssen et al. (2010), participants simultaneously grasped two bars and placed them into target boxes with either the left end or the right end of the bars pointing down. Although the majority of participants (59 %, n = 10) selected initial grasp posture in accordance with end-state comfort for both hands, the other participants (41 %, n = 7) did not, but rather selected grasp postures that were considered to be comfortable at the start of the movement.

Another study (Hughes, Seegelke, Reißig, & Schütz, 2012) examined whether grasp posture planning during a bimanual object manipulation tasks is influenced by the way the tasks goals are indicated. In this study, participants performed the same bimanual grasping in placing task as in (Hughes, Haddad, et al., 2011; Hughes, Reißig, & Seegelke, 2011), however, participants were assigned to one of three groups which differed with respect to how the required object end-orientations were cued. Specifically, for the first group (semi-symbolic cueing) the end-orientations were displayed as two-dimensional images of the objects (as in Hughes, Haddad, et al., 2011; Hughes, Reißig, & Seegelke, 2011), for the second group (symbolic cueing) they were displayed symbolically using orientation specifying letters (“L” for left, “R” for right, “O” for up, and “U” for down), and for the third group (direct cueing) the end-orientations were cued directly by illuminating the targets. Although the results of the semi-symbolic group replicated the results of previous studies (i.e., higher end-state comfort satisfaction for both hands during congruent as compared to incongruent object end-orientations Hughes, Haddad, et al., 2011; Hughes, Reißig, & Seegelke, 2011), notable inter-individual differences emerged for the other two groups. Specifically, in each of these two groups there was a subset of participants who grasp the objects using overhand grasps in virtually all trials regardless of condition.

The observation of the presence of inter-individual differences during goal-directed motor planning across a variety of different tasks provokes the question as to what factors might explain these differences. Attributing these differences to participants’ characteristics has not led to any meaningful insights. Specifically, neither gender (Hughes, Seegelke, Reißig, & Schütz, 2012; Hughes, Seegelke, & Schack, 2012; Rosenbaum et al., 1990, 1996), age (Hughes, Seegelke, Reißig, & Schütz, 2012; Hughes, Seegelke, & Schack, 2012), size (Rosenbaum et al., 1990), apparent strength (Rosenbaum et al., 1990), experimenter’s experience (Rosenbaum et al., 1996), nor direction of rotation (Rosenbaum et al., 1996) could account for the different strategies employed. Similarly, the differences reported in Chapter 3 and Chapter 4 cannot be readily explained by the factors age, gender, or participants’ height.

Alternative explanations based on perceptual and cognitive differences have been offered in order to explain the presence of inter-individual differences in motor planning. For example, Rosenbaum et al. (1996) suggested that participants who showed the end-state comfort effect in the handle rotation task despite the decreased precision demands at the end of the movement might have perceived the task to require more precise control at the end than was actually needed. This perception of precision, thus, lead the participants to the adoption of initial grasp posture that allowed for more control at the end of the movement. In addition, if a task requires high precision at both the start and the end of the movement, some participants may perceive the need for more precision at either location. Thus, participants would select a grasp posture that affords control at one of these distinct points in the task (i.e., either the start or the end of the movement Hughes, Seegelke, & Schack, 2012).

Furthermore, Janssen et al. (2010) have speculated that participants who select initial grasps that afford comfort at the start of the movement are 'less proficient planners'(p. 251). The authors bolster their argument with findings from participants with left congenital brain damage (Crajé, van der Kamp, & Steenbergen, 2009; Mutsaarts, Steenbergen, & Bekkering, 2006), who have shown comprised motor planning capabilities. However, counter to the proposed explanation by Janssen et al. (2010), it is conjectured that the absence of the end-state comfort effect in some participants does not necessarily imply that those participants have impaired motor planning capabilities. In the study of Mutsaarts et al. (2006), there were conditions in which inappropriate initial grasp selection would not allow participants to successfully complete the task (i.e., as these grasps would result in biomechanically impossible final postures), and hemiparetic cerebral palsy participants showed a large amount of such task failures, indicative of a planning deficit. However, participants in the other studies successfully accomplished the action goals of the task independent of the strategy employed. Moreover, counter to what one would expect from the precision hypothesis (Short & Cauraugh, 1999), the results presented in Chapter 4 demonstrate that both subsets of participants were highly accurate (as expressed through end orientation error) in doing so, rendering the less proficient planning hypothesis rather unlikely.

The suggestion that some participants will optimize comfort at the start of the movement is certainly in line with the results presented in the current thesis and those of other studies (Hughes, Seegelke, Reißig, & Schütz, 2012; Hughes, Seegelke, & Schack, 2012; Rosenbaum et al., 1996). For example, as delineated in Chapter 3, participants who did not adjust their initial grasp postures to the final targets might have prioritized initial-state over end-state comfort (recall that all participants optimized intermediate-state comfort in this task). Similarly, the results presented in Chapter 4 suggest that participants who rotated the object clockwise in the 180° rotation condition preferred end-state comfort, whereas participants who rotated the object counterclockwise preferred comfortable intermediate postures or averaged comfort. This latter suggestion again points to a potential drawback of studies that forced a binary grasp choice as in the critical conditions of those studies; participants can only adopt comfort at one location. As already acknowledged earlier, the results presented in Chapter 2 strongly suggest that if given the possibility participants will not strictly optimize comfort at one discrete position but rather distribute comfort across multiple locations (see also Herbort & Butz, 2010, 2012).

The findings that not all people show sensitivity (as expressed in initial grasp adjustment) to specific (future) task demands leaves room for different interpretations. Specifically, the tendency to select the same (or at least very similar) grasps irrespective of task demands might be an effective strategy to reduce the cognitive costs associated with movement planning (Hughes, Seegelke, Reißig, & Schütz, 2012; Hughes, Seegelke, & Schack, 2012). This concept has become popular under the label 'sequential effects'(Rosenbaum & Jorgensen, 1992) or motor hysteresis (Kelso, Buchanan, & Murata, 1994), but might also be involved in prospective motor control (Studenka et al., 2012). The idea is that action plans are not created from scratch for each movement, but that features of recently generated plans can be recalled and used for subsequent actions (e.g., R. G. Cohen & Rosenbaum, 2004; Jax & Rosenbaum, 2007; Rosenbaum & Jorgensen, 1992; Schütz et al., 2011; van der Wel, Fleckenstein, Jax, & Rosenbaum, 2007. That is to say, as long as a previously selected action can still be used to cope with the current task demands (considering biomechanical limitations), it might be re-used as much as possible and therefore obviates the need to create an entirely new action plan. Convincing experimental evidence for the cognitive origin of these effects has been obtained in the past (van der Wel et al., 2007). Recently, research has expanded this knowledge and strongly suggests that sequential effects result from a weighted function of the cognitive and mechanical costs of movement execution (Schütz & Schack, 2013).

With respect to the presence of inter-individual differences, involvement of similar mechanisms has been proposed. For example, Hughes, Seegelke, Reißig, and Schütz (2012) have suggested that the cognitive costs associated with visuomotor translation are higher for the symbolic and direct cueing conditions, and that participants adopted different strategies to cope with the task demands. Specifically, when the action goals are cued symbolically or directly, the stimuli do not provide information about the specific end-orientation. Thus, participants must transform the information from these stimuli into image-like representations of the objects (as in the semi-symbolic condition), and then plan their initial grasp postures accordingly. This process is thought to increase the cognitive costs associated with grasp posture planning. The authors speculate that participants who selected overhand grasps on virtually all trials tried to mitigate these costs by selecting a cognitively less demanding strategy. This hypothesis was supported by the kinematic data of the reach-to-grasp phase. Whereas reach-to-grasp times were longer for the incongruent conditions compared to the congruent conditions for participants who adjusted their initial grasp postures based on the specific object end-orientations, no such differences were found for the participants who always selected the same initial grasps, indicating that these participants already planned their grasp postures prior to stimulus presentation.

Similarly, participants in Hughes, Seegelke, and Schack (2012) who were not sensitive to the precision demands of the task, but instead always selected end-state comfort compliant grasp postures, might have reduced the cognitive costs by using previously successful grasps. That is to say, they adopted initial grasps that would lead to comfortable end-postures on the first few trials of the experiment. Given that these participants successfully accomplished the task goal without touching the target disk, they insisted in using these action plans, regardless of the precision demands of the task.

The results presented in Chapter 3 reinforce the interpretation that inter-individual differences might arise because some participants place more emphasis on the reduction of cognitive costs than others. Recall that in this experiment the initial grasp postures of those participants who did not adjust their grips to the final target orientations (but always selected similar initial grasps) were also very similar to their intermediate grasp postures (and close to the comfortable initial and intermediate postures) but resulted in final grasp postures that were considerably different from comfortable final postures. Consequently, these participants might have attempted to minimize postural transitions at early action segments (i.e., between the initial and intermediate grasp postures), and thus reduced the cognitive costs of changing movement plans. In addition, this strategy also ensured that they adopted comfortable initial *and* intermediate grasp postures for sacrificing comfortable postures at *one* - the final position - only.

All of the aforementioned explanations may be taken to suggest that inter-individual differences occurred because participants weighted action selection constraints differently, thus leading to different constraint hierarchies between participants. In other words, as the specific constraint hierarchies define the task as represented by the actor (Rosenbaum et al., 2013), it might be speculated that the differences arose due to in the way the tasks were cognitively represented (Rosenbaum et al., 1990). However, other than this speculation, the proposed suggestions do not offer much explanatory power. For the most part research has not addressed why people would weight action selection constraints differently, that is, what cognitive, biomechanical, environmental, contextual, or personal factors contribute to the presence of inter-individual difference during goal-directed motor planning.

In the field of cognitive psychology, individual differences are routinely addressed in the decision-making literature (see Appelt, Milch, Handgraaf, & Weber, 2011; Mohammed & Schwall, 2009, for reviews). Among others, this research has revealed that decisions that people make depend on factors such as past and future outcomes (Juliusson, Karlsson, & Gärling, 2005), personality traits (Brandstätter & Königstein, 2001; M. X. Cohen, Young, Baek, Kessler, & Ranganath, 2005; Smillie, Cooper, & Pickering, 2011), genetics (M. X. Cohen et al., 2005; Smillie et al., 2011), emotions (Bechara, 2004), and cognitive ability (Frederick, 2005). In contrast, given that those differences are rarely reported in motor control, those researchers apparently regard the presence of inter-individual differences as a nuisance, as just another source of unexplained variance. This view appears particularly puzzling given that it has been argued that making decisions about which movement to carry out is formally no different from any other kind of decision-making (Rosenbaum et al., 2001).

5.7 Toward a model of goal-directed motor planning

All things considered, it seems worthwhile to develop a model of goal-directed motor planning for grasping and placing actions, that not only incorporates the prevalent views and ideas of previous models (e.g., Rosenbaum et al., 2001; Schack, 2004), but also directly addresses the presence of inter-individual differences in motor planning and control. The proposed framework holds the view of a functional hierarchical organization of the CNS in which movements are first planned with respect to the action goals of a task. The action goals are considered to be at the top levels. These action goals, in turn, serve to guide the selection of lower-level action features (e.g., initial grasp posture planning), as well as the manner in which the task is performed (e.g., kinematics). Specifically, grasping and placing actions can be separated into an initial grasp and a transport component, within which there are a number of action selection constraints the system seeks to satisfy. The distinction between a planning and a control or execution component has already been proposed by Woodworth (1899), and is also supported by recent work (e.g., Hughes, Haddad, et al., 2011; Seegelke et al., 2011; Spiegel et al., 2012). For example, Hughes, Haddad, et al. (2011) examined how physically connecting two objects might influence bimanual grasping and placing movements to congruent or incongruent targets. The authors found that although object end-orientation congruency influenced both the grasping and transport component, physically connecting the two object altered only the degree of interlimb coupling between the hands (i.e., kinematics), indicating that task demands may not equally effect all levels. Both components, thus, are contingent upon the higher level action goals of the task and lower level action constraints. However, not all constraints might be equally important for each component. Consequently, for each component, the constraints are given weight factors and are ordered hierarchically according to their importance, leading to specific constraint hierarchies. The relative weighting of these constraints is supposed to be not fixed, but rather flexible and depend on contextual, conceptual, perceptual, environmental, cognitive, biomechanical, personal factors, forming task- and individual-specific constraint hierarchies. According to this view, inter-individual differences in task-performance are a result of variations in the relative order of action selection constraints between individuals.

One promising avenue to shed some light on how certain internal factors can predict task performance might be to examine links between cognitive representation structures and motor behavior. For example, one study (Stöckel, Hughes, & Schack, 2012) examined anticipatory motor planning using the bar-transport task and the development of cognitive representation of grasp postures in children aged 7, 8, and 9 years. In line with other studies on motor planning during childhood (see Wunsch, Henning, Aschersleben, & Weigelt, 2013, for a review) end-state comfort satisfaction increased with age, and the 9-year old children had distinct representation structures of grasp postures compared to the 7- and 8-year old children. Importantly, the sensitivity towards comfortable end-postures was related to the cognitive representation structure, such that children who had functionally well-structured representations exhibited a stronger preference for end-state comfort. These results strongly support the notion that cognitive action representations play an important role in the planning and control of manual action. In a similar vein, it seems worthwhile that future work should look at how advance planning capabilities are grounded in other contextual, conceptual, perceptual, environmental, cognitive, biomechanical, and personal factors. As a first step, it might be interesting to examine whether participants would exhibit similar specific strategies across several different motor tasks or whether the presence of inter-individual differences is rather highly task-specific. If the former holds true, a valuable next step would then be how individual-specific characteristics such as participants' metrics (i.e., biomechanical), working memory span, representation structure (i.e., cognitive), spatial visualization skills (i.e., perceptual) might predict participants' motor behavior and how these factors might interact with other task- and environmental factors. The ultimate goal of this approach would be to be able to predict and model task- and individual-specific constraint hierarchies that allow for successful motor task performance.

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6 Summary

Many of our daily activities require that we physically interact with one or more objects. Given that there is an infinite number of possible ways to achieve any given task, a core question in motor control is how particular actions for object manipulation are chosen. Previous research has demonstrated that the way people grasp objects is strongly influenced by future task demands or the intended action goal of the task. Anticipatory grasp posture planning has been extensively studies during object manipulation task composed of two action segments (i.e., grasp an object and one subsequent displacement), and a number of factors that consistently influence initial grasp choice (i.e., action selection constraints) have been identified. In contrast, surprisingly little work has considered action selection constraints during multi-segment object manipulation tasks.

The present thesis examined action selection constraints during grasp posture planning of multi-object manipulation tasks. Specifically, it focuses on the following action selection constraints and their interdependencies during multi-segment object manipulation tasks – (1) the tendency to select grasp postures that allow for control at later stages (end-state comfort effect), (2) the tendency to minimize postural transitions between immediately forthcoming and subsequent postures, and (3) a cognitive planning gradient, which indicates that action segments which occur earlier in a sequence are considered stronger in an action plan.

Chapter 2 assessed to what extent biomechanical and cognitive factors contribute to grasp posture planning during multi-segment object manipulation tasks, and whether participants would adjust their initial grasp postures over time. To this end, participants performed a grasping and placing task consisting of one, two, or three movement segments. The position of the targets was manipulated such that the degree of required object orientation between the home and the first target positions, and between the first and the second target positions, varied. Participants selected initial grasp postures that were inversely related to both the first and second target positions, suggesting that the multi-segment action sequences were planned holistically in advance, and that each element was considered during grasp posture planning. In addition, initial grasp postures were differently adjusted to the target positions depending on the temporal order in which the object was to be placed to these targets. During the initial stages of the experimental session initial grasp postures were influenced to a larger extent by the demands of the temporally proximal segment. However, over time, participants overcame these cognitive limitations and adjusted their initial grasp postures more strongly to the requirements of the temporally distal segment. Together, these results indicate that grasp posture planning is influenced by cognitive and biomechanical factors, and that participants learn to anticipate the task demands of temporally distal task demands, which reduces the burden on the central nervous system.

Chapter 3 examined the interplay between the tendency to select grasp postures that allow for comfortable or easy-to-control postures at later stages and the tendency to minimize differences between immediately forthcoming and subsequent postures during a three-segment object manipulation task. To this the experimental task introduced in Chapter 2 was modified such that the object orientation at the first (intermediate) target position was unconstrained, and participants were free to place the object in any desired orientation. On average, initial grasp postures were inversely related to final target orientation. In contrast, intermediate grasp postures were not influenced by final target orientation, but similar to the most comfortable postures obtained at this position indicating that participants selected initial grasp postures that afford control at the end of the movement sequence (end-state comfort) but also at the intermediate target position (intermediate-state comfort). Closer inspection of the data revealed the presence of inter-individual differences in initial grasp posture selection, ranging from very strong to virtually no adjustment. Strong adjustments in initial grasp postures led to more comfortable final grasp postures, whereas small adjustments led to less comfortable final postures. Interestingly, intermediate grasp postures were similar (and close to the most comfortable intermediate grasp postures) regardless of initial grasp posture adjustment. Consequently, it is proposed that participants who strongly adjusted their initial grasp postures to the final target positions planned the action sequence such that they adopted initial grasp posture that allow for more control at later stages. In contrast, participants who selected similar initial grips regardless of final target position might have aimed at minimizing postural differences between the initial and intermediate grasp postures as these were highly similar.

Chapter 4 examined whether participants would plan for comfort at later stages during a three-segment object manipulation tasks in which two objects are manipulated. In this task, participants opened a drawer, grasped an object from inside the drawer, and subsequently placed the object on a table in one of three different target orientations (0°, 90°, or 180° object rotation required). Results showed that initial grasp postures (i.e., when opening the drawer) were not influenced by the final target orientation, indicating that participants did not plan the entire movement sequence holistically in advance. In contrast, both the intermediate (i.e., when grasping the object) and the final grasp posture (i.e., when placing the object) were influenced by the final target orientation. In addition, inter-individual differences in grasp selection emerged for the 180° target orientation condition. Specifically, 42 % of the participants were able to successfully complete the action goal by adopting grasp postures that were comfortable at the intermediate but not the final position (intermediate-state comfort) and rotated the object counterclockwise. In contrast, 58 % of the participants preferred clockwise rotations and adopted grasp postures that allow for comfort at the end of the movement but not at the intermediate position (end-state comfort). These findings indicate that that participants might prioritize comfort at different stages in an action sequence, especially when larger degrees of object rotation are required.

In sum, the findings presented in this thesis demonstrate that multiple action selection constraints are considered and interact during the planning and execution of multi-segment object manipulation tasks. It is conjectured that action selection might be best understood as a process of ranking or weighting of constraints which are ordered hierarchically according to their importance. This ranking is assumed to be not static, but rather flexible and depend and depend on contextual, conceptual, perceptual, environmental, cognitive, biomechanical, personal factors, forming task- and individual-specific constraint hierarchies. According to this view, inter-individual differences in task-performance are a result of variations in the relative order of action selection constraints between individuals. A challenge for future work is how individual-specific characteristics might predict participants' motor behavior and how these factors might interact with other task- and environmental factors.

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