

Kinematics and control of precision grip grasping

Inaugural-Dissertation
zur Erlangung des akademischen Grades
Doctor rerum naturalium (Dr. rer. nat.)
an der



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vorgelegt am 6. September 2010
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Zusammenfassung

Diese Dissertation handelt von den Mechanismen mit denen unser Zentralnervensystem menschliche Feinmotorik koordiniert.

Gegenstand der ersten beiden Projekte ist die Theorie von A. D. Milner und Goodale (1995). Laut diesen Autoren gibt es im visuellen System zwei unabhängige Verarbeitungspfade. Der *dorsale* Pfad verarbeitet visuelle Information zum Zweck der Handlungssteuerung. Der *ventrale* Pfad vermittelt bewusste visuelle Wahrnehmung. Beide Pfade verfügen über teils unterschiedliche Anteile der gesamten visuellen Information. So soll der dorsale Pfad gegenüber dem ventralen zum Beispiel durch geringere Farbsensitivität sowie einen schnelleren Zerfall der Information gekennzeichnet sein.

Im ersten Projekt wurde die Eignung von Farbinformation zur Handlungskontrolle getestet. Teilnehmer der Studie griffen nach farbigen Stimuli deren Helligkeit variiert wurde. Einige der Stimuli hatten die gleiche Helligkeit wie der Hintergrund vor dem sie präsentiert wurden. Diese Stimuli hoben sich also nur durch ihre Farbe vom Hintergrund ab. Trotz der angenommenen Farbinsensitivität des dorsalen Pfades konnten unsere Teilnehmer auch diese Stimuli problemlos greifen.

Gegenstand des zweiten Projektes waren die Unterschiede beider Pfade im zeitlichen Verfall der visuellen Information. Einigen Patienten mit speziellen Hirnschädigungen soll es möglich sein zwischen den Repräsentationen beider Pfade zu wechseln. Diese *optischen Ataktiker* zeigen starke Unsicherheit bei visuell geführten Bewegungen wie Zeigen oder Greifen. Wiederholt wurde jedoch gezeigt, dass ihre Bewegungen genauer werden wenn die Ausführung einige Zeit nach der Zielpräsentation erfolgt. Himmelbach und Karnath (2005) berichten, dass diese Verbesserung beim Zeigen linear mit der Länge des zwischengeschalteten Intervalles zunimmt. Wir versuchten dieses Ergebnis zu reproduzieren und auf das Greifen zu generalisieren. Die zwei von uns gemessenen Patienten zeigten beim Greifen jedoch keinen Effekt. Beim Zeigen zeigte sich eine Verbesserung nur bei einem Patienten und nur in einem von mehreren Maßen für die Zeigegenauigkeit.

Insgesamt betrachtet widersprechen die Ergebnisse des ersten und zweiten Projektes der Vorstellung zweier getrennter visueller Pfade. Die hier präsentierten Daten lassen sich ebenso effektiv, aber deutlich effizienter, durch die Verarbeitung in einem einzelnen visuellen Verarbeitungspfad erklären.

Das dritte Projekt soll eine Lücke in bestehenden Modellen zur Beschreibung der Kinematik des Greifens schließen. Alle diese Modelle sind darauf angewiesen, dass ihnen die Zielpunkte der Bewegung vorgegeben werden. Aus der Literatur zu menschlichem und maschinellm Greifen extrahierten wir die plausibelsten Regeln zur Auswahl dieser Zielpunkte. Wir brachten diese Regeln experimentell in Konflikt zueinander und schätzten auf diese Weise ihren relativen Einfluss. Das Modell wurde anschließend validiert indem wir die besten Greifpunkte für einen neuen Satz von Objekten vorhersagten. Mit wenigen Regeln konnten wir so sehr erfolgreich im Vorhinein die vom Menschen präferierten Greifpunkte bestimmen.

Abstract

This thesis is about the kind of signals used in our central nervous system for guiding skilled motor behavior.

In the first two projects a currently very influential theory on the flow of visual information inside our brain was tested. According to A. D. Milner and Goodale (1995) there exist two largely independent visual streams. The *dorsal* stream is supposed to transmit visual information for the guidance of action. The *ventral* stream is thought generate a conscious percept of the environment. The streams are said to use different parts of the visual information and to differ in temporal characteristics. Namely, the dorsal stream is proposed to have a lower sensitivity for color and a more rapid decay of information than the ventral stream.

In the first project the role of chromatic information in action guidance was probed. We let participants grasp colored stimuli which varied in luminance. Critically, some of these stimuli were completely isoluminant with the background. These stimuli thus could only be discriminated from their surrounding by means of chromatic contrast, a poor input signal for the dorsal stream. Nevertheless, our participants were perfectly able to guide their grip to these targets as well.

In the second project the temporal characteristics of the two streams were probed. For a certain group of neurological patients it has been argued that they are able to switch from dorsal to ventral control when visual information is removed. These *optic ataxic* patients are normally quite bad at executing visually guided movements like e.g. pointing or grasping. Different researchers, however, demonstrated that their accuracy does improve when there is a delay between target presentation and movement execution. Using different delay times and pointing movements Himmelbach and Karnath (2005) had shown that this improvement increases linearly with longer delay. We aimed at a replication of this result and a generalization to precision grip movements. Our results from two patients, however, did not show any improvement in grasping due to longer delay time. In pointing an effect was found only in one of the patients and only in one of several measures of pointing accuracy.

Taken together the results of the first two projects don't support the idea of two independent visual streams and are more in line with the idea of a single visual representation of target objects.

The third project aimed at closing a gap in existing model approaches on precision grip kinematics. The available models need the target points of a movement as an input on which they can operate. From the literature on human and robotic grasping we extracted the most plausible set of rules for grasp point selection. We created objects suitable to put these rules into conflict with each other. Thereby we estimated the individual contribution of each rule. We validated the model by predicting grasp points on a completely novel set of objects. Our straightforward approach showed a very good performance in predicting the preferred contact points of human actors.

Contents

1	Introduction	1
1.1	Significance of the grasp behavior	2
1.2	The anatomy of the grasp effector system	5
1.3	The spinal cord level of processing	9
1.4	The subcortical level of processing	11
1.5	The neocortical level of processing	13
1.6	Models of grasping	25
2	Grasping isoluminant stimuli	37
2.1	Introduction	38
2.2	Methods	42
2.3	Results	46
2.4	Discussion	50
3	Delayed pointing and grasping in optic ataxia	55
3.1	Introduction	56
3.2	Method	60
3.3	Results	64

3.4	Discussion	71
4	A model on human grasp point selection	83
4.1	Introduction	84
4.2	Results	88
4.3	Discussion	96
4.4	Method	99
5	Discussion	103
5.1	Conclusions and outlook from chapters 2 and 3	104
5.2	Conclusions and outlook from the grasp point selection model	109
	References	117

Chapter 1

Introduction

I have always thought the actions of men
the best interpreters of their thoughts.

John Locke

Observing human actions is a key method to unravel the mysteries of our brain. We can understand the human central nervous system, with the neocortex at the very top of its hierarchy, as an information processing system mapping sensory inputs to motor outputs. If we observe actions which are caused by well defined sensory inputs we can measure the dependencies and independencies in the system in order to develop and subsequently test formal models describing it. Although this approach does not necessarily provide us with a correct insight of how information is processed inside the system, in the first place often a prediction of the outputs is what is needed or wanted initially. Also, starting with the development of the electroencephalography (EEG) by Berger (1929) several methods like the magnetoencephalography (MEG), positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) have been devised for observing the working brain directly. By combining the knowledge of sensori-motor mappings from behav-

ioral studies with confirmed knowledge about structural and functional relations in the brain gained from other methods we are able to draw further conclusions about how exactly a certain task is solved.

In this thesis the act of human grasping is taken as the observable behavior which is measured in order to gain a deeper insight into the formal relations between sensory input and motor output and about the brain structures possibly mediating this mapping. In chapters 2, 3 and 4 I will present three projects with experimental research designed to advance our knowledge in the domain of control of human hand movements. Prior to these chapters the remainder of this introduction will give the foundation on which the presented research is based upon. I will firstly emphasize the particular importance the grasp movement has for us as human beings which makes it an excellent subject for studying the organizing principles of the nervous system. Afterwards I will sketch a scheme of the musculo-skeletal anatomy carrying out grasp movements and the different layers of neuronal processing guiding them. Lastly I will introduce some influential ideas which have been devised in order to describe and understand how this amazing ensemble of bones, muscles, tendons and neurons is orchestrated. Chapters 2,3 and 4 are all preceded by their own short introduction which is sufficient to understand their content. The hurried reader thus might also skip the general introduction and directly proceed to the chapter of interest.

1.1 Significance of the grasp behavior

More than half a century ago Napier (1956) laid the foundation of today's research in grasp movements by establishing a very simple but compelling classification of the pattern of grasp behaviors the human hand is capable to perform. He proposed that a fundamental distinction exists between two kinds of patterns: On the one hand, we are able to form a *power grip* where the thumb presses an object against

the remaining fingers and the palm. On the other hand we can do a *precision grip* where the pads of the thumb and one or more other digits are used to pinch an object between them (see figure 1.1).

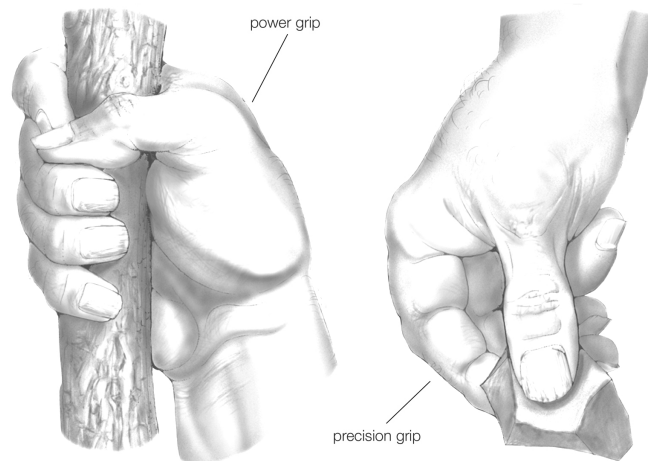


Figure 1.1: Power (left) and precision (right) grip. Adapted from Encyclopædia Britannica, 2010.

We as human beings share the principal ability of grasping in the broadest sense with several other species. Animals as different from us as for example the panda bear *ailuropoda melanoleuca* or the mantis (e.g. *sphodromantis viridis*) are able to oppose actuators of their limbs and thus clamp things between them. Even chimpanzees (*pan troglodytes*), however, which are our closest genetic relatives (Ruvolo, 1997), have hands lacking several of the features which make the human hand so versatile. For instance, since our evolutionary path diverged from that of the chimpanzees we developed broad apices on the proximal phalanx of each finger, a prolonged thumb, three new muscles for the control of it and the remaining digits shortened and straightend (Young, 2003). These and some other modifications (see Tocheri, Orr, Jacofsky, & Marzke, 2008 for a more extensive list), although they might seem to be small at a first glance, were in fact very radical. While for humans the typical pad-to-pad opposition grip of index finger and thumb is a preferred way of grasping small things in chimpanzees the different anatomy makes this grip

relatively insecure and thus a very much less preferred alternative (Marzke, 1997; Butterworth & Itakura, 1998). Indeed it has long been believed that chimpanzees aren't capable of using this grip at all (Butterworth & Itakura, 1998).

But why is the precision grip such an important feature of the human hand? As Marzke (1997) points out the precision grip greatly enhanced our ancestors' ability to create new tools. It is not completely clear of what nature the first tools might have been. Young (2003) for example promotes the hypothesis that it were hand held weapons which granted the holders an evolutionary advantage. It is obvious, however, that tool use is one of the major foundations of the development of culture as it allows the individual to deal with the surrounding environment in a new way and with a much greater amount of control about it. Some authors even hypothesize that another important foundation of our culture—language—is in its phylo- and ontogenetical development very tightly coupled with the development of tool use (Greenfield, 1991). Therefore the subtle anatomical redesign of our hand, which equipped us with the ability of precision grip grasping, in the end might be the foundation of our very culture at large. Traces of the importance of grasping for our cognitive development are still present to the day. In many languages words which describe that something is understood have developed from roots related to grasp words like for example in the Italian language *capire* (understand) from the Latin *capere* (grasp, seize), the French, Spanish and Italian word *comprendre*, *comprender*, *comprendere* from the Latin *comprehendere* (take firmly, seize) or the German *begreifen* from the German root *Griff* (grip) as Dworkin (2006) points out. This author even makes a special point in stating that the inverse transfer of meaning, i.e. *understand* \rightarrow *grasp*, does not occur.

These reasons make grasping—and particularly precision grip grasping—a behavior which has a great potential for revealing to us very basic principles underlying the modes of operation of the human brain.

In the following sections an overview of the structures involved in human grasping will be given. The purpose is to sketch an idea of the interplay between the different

components involved. We will start at the low level of the bones and muscles of the the human arm, and ascend through the structure of the spinal cord and the supraspinal but subcortical stages of processing all the way up to the level of the neocortex. A special emphasis then will be placed on models describing the flow of information on the neocortical level particularly some instances of the *two-visual-systems* hypothesis which has been a very influential model of structure and workflow in the last decade and has inspired much of the research presented in this thesis.

1.2 The anatomy of the grasp effector system

In most everyday tasks human grasp movements involve at least the movement of the complete arm. Caronni and Cavallari (2009) moreover showed that even simple movements of a single digit are preceded and accompanied by subtle involuntary motor adjustments in the rest of the arm. The according muscles are synergistically activated for preparation of the movement and in order to counteract the resulting torques for the maintenance of overall stability. This pattern is of course also found with respect to the whole body for movements of the complete arm (cf. Wing, Flanagan, & Richardson, 1997). It develops with advancing age (Hay & Redon, 2001). Involuntary adjustments like these are the foundation for all other movements. However, as we are more strongly interested in the processing taking place at higher levels of the central nervous system (CNS) subsequently the focus will be mainly on the intentional movements of the arm.

Movements of the human arm can be described in a variety of reference frames or coordinate systems. From an anatomical perspective joint space is a particularly reasonable choice although there is evidence that it is not used by the CNS for planning movements (Shafir & Brown, 2010). In joint space every movement consists of a change of angles in the involved joints over time. Every combination of joint angles, that is every point in joint space, is called a posture. How complex a movement

can get depends on the available degrees of freedom in the participating joints. If we disregard the nearly amobile joints between the eight carpal bones and between the distal carpal bones and the metacarpal bones of digits II-V we still have to deal with a system of as many as 27 degrees of freedom in the human arm: three in the gleno-humeral shoulder joint, one in the humero-ulnar joint, one in the proximal and distal radio-ulnar joints, two in the radio-carpal joint and four in each digit. In the digits we find a non-rotatable ball joint with two degrees of freedom at the basis of digits II-V and two anatomical ball joints which are functional hinge joints between proximal and medial phalanx and between medial and distal phalanx respectively. In digit I, the thumb, we find a saddle joint at the articulation carpo-metacarpalis I (pollicis). This type of joint is found exclusively at this place in the human body and had a distinct evolution since human and ape development parted as the articular surfaces are relatively flat in the modern *homo* (see Tocheri et al., 2008 for a detailed account on the evolution of human hand features). It is this construction along with the new muscles (as mentioned on page 3) which enables the opposition of the thumb to the other digits and the application of forces allowing for a secure precision grip. There are two more joints in the thumb which are functional hinge joints just as in the other digits. The thumb thus consists only of two phalanges, one less than the rest of the digits. Still its flexibility is the basis of our grasp behavior and, as was pointed out above, probably the basis of large parts of our culture.

In order to generate a movement in the joints we need muscles exerting the force and providing the dynamic movement range. Also we need tendons connecting muscle and bones at origin and insertion. In the human arm and hand we find a total of 51 muscles. The patterns of connections between muscles and bones shows that some joints cannot be moved independently by a particular muscle but will covary in joint space with other joints. In total we find a highly complex designed effector organ where different muscle activation patterns can lead to the same posture. That means that the joint space outcome of a muscular activation input is overdetermined. Moreover a certain posture must be achieved by a movement which in

principle consists of a smooth transition between an infinite number of postures. It is obvious that there is a vast amount of possible movement paths leading from one particular posture to the other, even if we restrict the amount of time available for the movement and consider the temporal dynamics of muscles and tendon tissue. These dynamics, which have to be taken into account when the CNS is planning a movement, can only be captured by relatively complex non-linear models (Hartung, 1975; Zajac, 1989). Rather simple spring models, however, can often give a very good approximation to the dynamics of a system of muscles, tendons and bones. A very influential muscle model of this type was proposed as early as the first half of the last century by Hill (1938). With a straightforward approach (see fig. 1.2) this author could very well capture the dynamic properties of the muscle and his work is still the basis of modern, more sophisticated, approaches to the problem (see for example Ettema & Meijer, 2000). In figure 1.2 (panel c) we see a typical example of how muscle properties (e.g. velocity of shortening) depend non-linearly on task demands. In chapter 4 it will be demonstrated how such nonlinearities can be used in order to build a physiologically plausible model on grasp point selection. Models of muscles and complex multi-muscle systems like the elbow joint (Fisk & Wayne, 2009) or the shoulder (Favre, Snedeker, & Gerber, 2009) are utilized for example to predict the expected improvement in functionality prior to joint surgery. It must be taken into account, however, that the dynamics of the tissue may differ between different specimen of muscles and tendons (Cui, Maas, Perreault, & Sandercock, 2009). Even for one particular muscle differences can be found between individuals (Winter & Challis, 2010). Differences are also found between age groups, but interestingly not between sexes (O'Brien, Reeves, Baltzopoulos, Jones, & Maganaris, 2010).

For online motor control not only the efferent signal, bringing information from the CNS to the muscles, is needed but also feedback about the current state is necessary. This is information about muscle length and change of muscle length from the neuromuscular spindle, about tendon tension from Golgi tendon organs and about joint stance and change of joint stance from the Ruffini and Pacinian

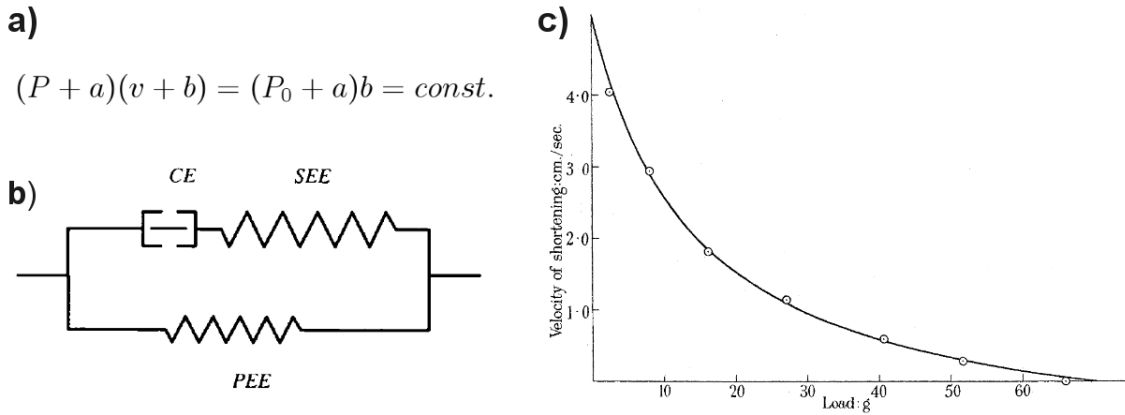


Figure 1.2: Overview of the Hill model. **a)** Formalized description of the muscles state relating load P to velocity of contraction v with P_0 being the muscles maximal tension and a and b constants. **b)** Visualized Hill-type model consisting of a contractile element (CE), a series elastic element (SEE) and a parallel elastic element (PEE). Reprinted from Ettema & Meijer (2000). **c)** Non-linear relation between load and contraction velocity. Circles represent measurements from a muscle specimen, the line depicts the relationship according to the model. Reprinted from Hill (1938).

corpuscles. The importance of these informations in the guidance of motor actions is evident by the fact that some of their fibers belong to the fastest class of all nerve fibers, with a speed of transmission of up to $120 \frac{m}{s}$ (Schmidt & Thews, 1990, pp. 40,90-93).

Modeling the spatial and temporal dynamics of this complex assembly rightfully seems to be a daunting task. Evidence that the CNS does not necessarily have to deal with all of the complexity comes from an experiment of Polit and Bizzi (1978). They demonstrated that—when using a simple spring-like muscle model—all that must be controlled by the CNS for the execution of accurate hand movements to visual targets is a single variable. They did so by measuring pointing movements of monkeys who could not see their own movements prior to and after removal of sensory information from the proprioceptors by means of denervation. The monkeys were able to accurately acquire the target before and also after surgery and even if

the pointing arm was displaced just prior to trial initiation. From these data the authors concluded that all that is controlled is the desired equilibrium point of the whole agonist/antagonist muscle system. When the cortical control flow for guiding grasp movements shall be modeled it is thus a physiologically plausible approach to abstract from the activation of single muscles and stick to a few control variables which are monitored during the movement. This approach has been used in several models of grasping as will be outlined in more detail below in section 1.6.

1.3 The spinal cord level of processing

The signals coming from the receptors of the muscles and joint capsules travel along their specific nerve fibers into the spinal cord. In the spinal cord they are switched to the next neuron which is the first neuron belonging to the CNS. This switch is the first possibility for accessing and modulating the afferent signals. Just as the sensory inputs are switched here, also the efferent outputs are: The spinal cord contains the motoneurons which are connected to the myoeceptors of the muscles. Neither the pyramidal tract, which carries signals from the primary motor cortex located in Brodmann's area 4 (BA4), nor the extrapyramidal fibres from the nuclei vestibulares, nucleus ruber, formatio regularis and the oliva are reaching the muscles directly. All of this information is switched to motoneurons of the spinal cord.

From this switching arises the spinal cords property of being an own layer of processing. The computations done here can be seen as the foundation the more filigrane aspects of motoric control are built upon. Via the reflexes the spinal cord adjusts the tone of the muscles and mediates quick, unconscious reactions like the withdrawal of the digits from e.g. a cup which is too hot for grasping. It also minimizes the amount of input needed from supraspinal structures for the execution of a motor plan. In their review on experiments mainly done in frogs, rats and cats Bizzi, Cheung, d'Avella, Saltiel, and Tresch (2008) picture a modular view on motor

control. Here the spinal cord is proposed to be in possession of a set of basic *synergies*—motor activation patterns of a small set of muscles which produce a certain motor outcome. These synergies can be combined by supraspinal structures. The authors stress the comparison with the alphabet where single letters can be combined to words or words to sentences. In a similar fashion complex movements would arise from the combination of these “motor letters”. A comparison can also be drawn to *geons* which have been proposed to be the building blocks of our visual perception (Biederman, 1987). Grillner, Wallén, Saitoh, Kozlov, and Robertson (2008) propose a similar modular architecture where the output of spinal *central pattern generators* can modularly be combined to produce locomotor behavior. Although experimental investigations of these authors come from the lamprey they demonstrate that by extension of the proposed networks the principle is applicable to the limbs of other vertebrates as well. Generally speaking, assessment of the functions of the human spinal cord in isolation of course is far more difficult to do than in the animal model. There is, however, no strong indicator why the general mechanisms of other vertebrates should not be applicable to the human. In a study with individuals suffering from complete spinal cord injury Harkema (2008) also showed experimentally that the human spinal cord contains generators for locomotor patterns as well. These findings give rise to an exciting outlook for the future: If we would be able to understand this alphabet of human motor letters it could be possible to artificially elicit complete motor patterns like e.g. walking in individuals suffering from spinal lesion as e.g. Barbeau et al. (1999) suggested. Up to now, however, research into this field has been focused mostly on rhythmic motor patterns. Barbeau et al. recognize that it is unclear if circuitry for non-rhythmic patterns like reaching exists in the spinal cord. If this would be the case, however, it could be possible that we could even access the motor alphabet in order to produce arbitrary complex, non-rhythmic movements. Yet, for this task what would be needed is a thorough knowledge of the input which normally reaches those spinal centers from the higher neural structures. Developing models of human movement guidance, like the ones presented later in

this introduction and the one developed in chapter 4 of this thesis, is a first step in this direction.

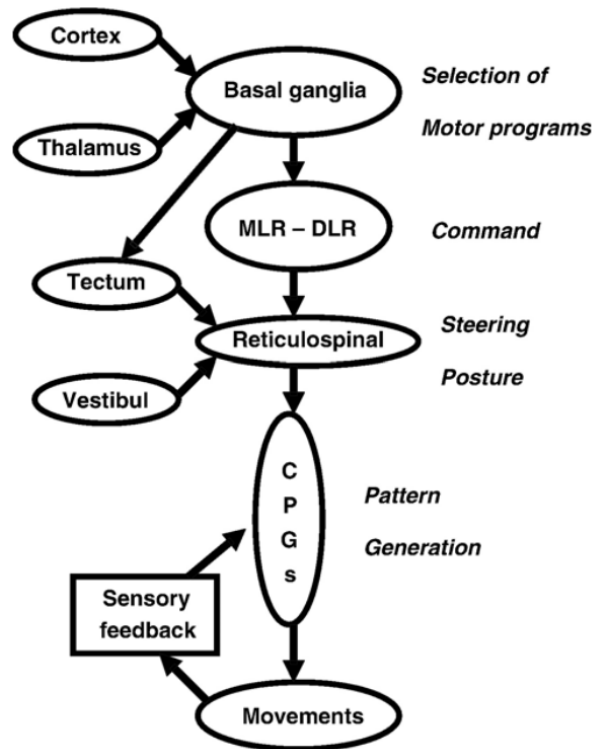


Figure 1.3: Modular model for motor control reprinted from Grillner et al. (2008). Simple motoric patterns can be generated within the central pattern generators (CPGs) of the spinal cord. These modules are controlled in turn by supraspinal structures which will be addressed in the following sections. DLR and MLR refer to the diencephalic and mesencephalic locomotor region respectively.

1.4 The subcortical level of processing

Coming from the spinal cord the sensory information from the proprioceptors enters subcortical structures at different sites. Much of it enters the cerebellum where it takes part in the process of balancing the whole body and is used for the build up of a representation of the body posture which can be used to coordinate and fine-

tune the “neuronal blueprints” of a movement from the motor cortex (Trepel, 2004, pp. 162-164). The latter is needed for checking if a certain motor plan can reasonably be carried out from the actual posture (Trepel, 2004, p. 164). The cerebellum is important for motor learning and also plays a crucial role in grasping: T. E. Milner, Franklin, Imamizu, and Kawato (2007) using fMRI could show that both, a simple and a complex grasp and hold task elicited activation in the ipsilateral cerebellum. The activation, however, was found in more loci and also in a much more widespread pattern in the complex task. Aside from its motor functions the cerebellum may very generally play a part in different associative learning tasks, like for example fear conditioning, as Timmann et al. (2009) report.

A typical symptom resulting from damage in the cerebellum is ataxia, a condition of gross movement coordination failure. It heavily impairs movement patterns like locomotion, pointing and grasping. The impairment is of both, spatial as well as temporal nature as the cerebellum is also very much involved in the temporal coordination or coupling of actions. A lack of this functionality of temporal coupling leads to the symptom of *adiadochokinesia* which is an inability to smoothly activate agonists and antagonists for example in a screwing-like hand movement. Ataxia as a symptom may also result from lesions to other loci of the CNS. In the project presented in chapter 3 of this thesis data of two patients suffering from *optic ataxia* are presented. This condition is due to lesion in areas of the parietal cortex. The result, though, is also an impairment in movement coordination.

Another part of the proprioceptive information reaches the thalamic nucleus ventromedialis via the medial lemniscus. From here the information reaches the postcentral gyrus (BA3, BA2 and BA1) where it is integrated into a conscious perception of the state of muscles joints and limbs (cf. Jones & Porter, 1980). The thalamus, however, is also important in integrating information from the cerebellum and the basal ganglia. It in turn projects to the primary motor cortex and gives the *go* signal for a movement start (Trepel, 2004).

The basal ganglia are supposed to have a filtering function for the execution

of motor plans (Trepel, 2004; Grillner et al., 2008). As the cells of their input layer—the striatum—have a high threshold for excitation they prevent many of the motor plans proposed from the cortical level to come to realisation (Grillner et al., 2008). Lesions to structures of the basal ganglia lead to either hypo- or hyperkinesia. For example we find akinesia as a cardinal symptom in individuals suffering from Parkinson’s disease, a condition associated with a decrease in cell numbers in the substantia nigra, which is a part of the basal ganglia. Hyperkinesia contrariwise is found in individuals with ballism and Huntington’s disease which also are associated with dysfunction in the basal ganglia. More recently also the condition of attention deficit hyperactivity disorder (ADHD) was linked to the basal ganglia, namely to abnormal functioning in the striatum (Uhlíkova et al., 2007; Durston et al., 2008). In ADHD individuals are hyperactive not only with respect to their motor behavior but also on a cognitive level and thus exhibit difficulties in focusing on a task.

Of course there are several more subcortical sites involved in the planning and execution of movements. For the sake of shortness only some of the most important have been discussed here. The work presented in chapter 4 of this thesis may prove to be of significance especially in the context of some of the presented disorders. It will be shown there how movements of healthy persons can be modeled. This approach may also disclose possibilities for the assessment of abnormal functioning. In the next section we will now deal with the top of the control hierarchy, the neocortex.

1.5 The neocortical level of processing

As we have ascended all the way up from the muscles via the peripheral nerves, the spinal cord and the subcortical structures we now arrive at the neocortical level. With regard to motor control the neocortex is just the mere tip of the iceberg as we have seen that a vast amount of work is already done subcortically. However, in our strive for understanding human actions the neocortical level certainly has been

and still is a focus of attention. One important reason is because it is here where our conscious decisions about actions are made.

In the following sections first an overview about the most important cortical areas involved in the control of grasping will be given (see also the overview given by Hesse (2008) pp. 17–20). Then it will be outlined how visual information enters the brain and via which routes it reaches areas involved with motor control. Finally we will enter the controversial field of how exactly the visual information is used to guide actions. A short review on some of the most influential theories related to this topic will be given.

1.5.1 The cortical areas of proprioceptive perception

If we first follow the path of the proprioceptive sensory input as we have done in the preceding sections we find that their projections go from the thalamic ncl. ventromedialis up to the postcentral gyrus or somatosensory cortex consisting of BA3, BA2 and BA1. Here they are used for establishing a percept of body posture. The perception of ones body, however, is very complex and involves a lot of cortical regions. Berlucchi and Aglioti (2010) give a short overview on the topic of the body representation which is an unresolved issue producing an ongoing debate since Head and Holmes (1911) first introduced the concept of the *body schema*.

1.5.2 The cortical areas of grasping and motor control

The primary motor cortex Directly adjacent to the postcentral gyrus in the rostral direction lies the precentral gyrus, BA4, which contains the *primary motor cortex* (also called M1). Neurons in this part of the brain are responsible for the input to the α - and γ -motoneurons of the spinal cord and to the motoric brainstem nuclei. M1 receives its input mainly from the thalamus. Its role is the execution of a movement which was prepared before in areas like the premotor cortex and the cerebellum and has passed the filter of the basal ganglia. The neurons in the primary motor cortex do not excite single muscles but code for movement patterns (Poeck

& Hache, 2001, pp. 110-112). In the context of a modular organisation of the motor system like it was proposed by Bizzi et al. (2008) and was circumstantiated with data from stroke patients (Cheung et al., 2009) M1 would be the entity combining the spinally coded motor letters into words—that is the spinal muscle synergies into purposeful movements. Very well controlled experimental evidence on how lesions to M1 impair fine hand movements comes from a study in the macaque monkey conducted by Darling et al. (2009). These authors also show how quickly hand function can recover which is an indication of the high plasticity of the brain. The corticospinal tract which carries the efferent signals from M1 to the spinal cord is a phylogenetically recent development as it is exclusively found in mammals. It is also not fully functional at birth, its maturation continuing until the second year of infancy (Poeck & Hache, 2001). The relatively clumsy grasp attempts seen in the early infant are partly due to this immaturity of the cortico-spinal system.

The premotor cortex The premotor areas are located rostrally to the primary motor area in BA6 and part of BA8. The medial and apical parts of them are called *supplementary motor cortex* (SMC). The SMC is involved in the planning of motor actions and has the role of a motoric memory from which action patterns can be selected (Trepel, 2004, p. 217). Anatomically we find in the premotor cortex extensive indirect connections with the cerebellum via the subcortical structure of the pons which are needed for the fine tuning of motor plans.

Although exactly how a motor plan is encoded as a chunk in the premotor cortex remains elusive to the date researchers have already gained some crucial insights. Many studies on this topic make use of animal relatives of the human in order to exploit the expanded experimental possibilities for drawing conclusions about brain function. Much research in the following decades was inspired by a study of Rizzolatti et al. (1988) who demonstrated that the neurons in the rostral inferior BA6 (macaque area F5) are selectively active during certain types of actions. Among these neuron clusters were also neurons which were found to be selective for precision

grip grasping but not the other observed behaviors like e.g reaching. Rizzolatti et al. (1988) classified the neurons in this brain area into a *proximal* and a *distal* class depending on the action they were related to. They found the majority of neurons in F5 to be related to distal movements, for example grasping. Gentilucci et al. (1988) demonstrated that many neurons of the macaque area F4, which is the caudal part of inferior area 6, in turn are more responsive for proximal movements like reaching. These and similar findings were seen by some researchers to support the idea that a grasp movement consists of and is planned in terms of reaching and grasping more or less separately. A more detailed account on these models will be given below.

The quest on finding out what is coded in the premotor areas and how it is coded continues to the day. Recently Umiltà et al. (2008) for example could show that neural activity here is not restricted to grasp movements with the hand but is also present in grasping with tools. These findings indicate that these areas comprise a very general, effector-unspecific, concept of movements. They may rather code the goal of the intended behavior instead of the actual way of achieving it. Note, however, that Jacobs, Danielmeier, and Frey (2010) using fMRI and behavioral data in human participants demonstrated that also effector-specific representations probably co-exist in the homologue regions of the human brain.

Only four years after the influential findings of Rizzolatti et al. were published researchers from the same group reported another striking feature of the macaque premotor cortex: di Pellegrino, Fadiga, Fogassi, Gallese, and Rizzolatti (1992) showed that some neurons from this region are even active during the mere observation of the action they code for. The finding of these *mirror neurons* has inspired a great deal of research far beyond the field of motor control. Relatively early they were associated with our language capabilities as Rizzolatti, Fadiga, Gallese, and Fogassi (1996) related the premotor areas in the macaque to Broca's area, the human locus of speech production and proposed that language might have emerged from a more action-oriented way of communication with gestures. Recently Corballis (2009) outlined a theory on how language might have gradually evolved from man-

ual gestures and summarizes evidence from data in the human. Research on mirror neurons produced general insights on our social interactions, empathy with others and understanding their intentions and it still continues to do so. The discovery of these neurons was so influential that Ramachandran (2000) in a famous quote predicted that “mirror neurons will do for psychology what DNA did for biology”. With regard to motor control Jeannerod (2001) issued the *simulation theory* where he proposed that our executed actions are just one end of a continuum which ranges from covert—or simulated—to overt behaviour. In this context it is of interest that Raos, Evangeliou, and Savaki (2004) were able to show mirror neuron activity in the rhesus monkey even in areas as basic and near to the end-effector as the primary motor and sensory areas.

The parietal lobe The parietal lobe extends between the occipital lobe—which contains visual areas—and the central sulcus, the border to the frontal motor areas. As we will see this spatial relations also are in correspondence to the function as therein visual information is transformed in several ways for its use in action plans.

The intraparietal sulcus (IPS) subdivides the parietal lobe into a superior parietal lobule (SPL) and an inferior parietal lobule (IPL). The IPS itself, however, can be regarded as a functional unit as well. Its anterior part, area AIP has been subject to extensive research and together with macaque area F5 it is regarded as a crucial circuit for grasping where F5 codes for specific motion phases while in the parietal areas many neurons were found to be active during the whole motion (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Fagg & Arbib, 1998). Jeannerod et al. (1995) proposed that the parietal areas are responsible for the transformation of the visual input about object properties like size and orientation into a reference system for selecting an appropriate grasp. This proposition is supported by recent evidence as Srivastava, Orban, Mazière, and Janssen (2009) found that AIP in the macaque also makes use of visual disparity information for coding the shape of objects which is a necessary pre-processing step for grasping.

The superior lobule of the parietal lobe is involved in the control of grasp movements as well. Based on their data from macaque monkeys performing different kinds of grips Fattori et al. (2010) concluded that neurons in area V6A—like AIP neurons—are sensitive to distal properties of the grip, like for example wrist orientation, but additionally also code for the reach direction of the arm, a proximal aspect of the movement. They propose that these neurons might be part of a second grasp network which exists alongside the AIP–F5 network and might play an important role particularly in fast-controlled grasp actions.

Just as in the other parietal areas we find a lot of action and grasp related processing taking place in the inferior parietal lobule (IPL) as well. A specialty of these areas in the macaque seems to be that they discharge differently depending on what manipulation is following a particular action. This was observed for example by Fogassi et al. (2005) when comparing a movement which brought an object to the mouth versus a movement where the object instead was placed somewhere else. These authors also showed that there is a considerable quantity of mirror neurons present in this area. Taken together these findings give rise to the assumption that neurons of this cortical region help the animal to infer the intention of another individuals' actions. Another very interesting finding regarding the role of the IPL in the human was reported by Peeters et al. (2009). They found a region in rostral IPL specifically active in the human but not the monkey participants of their study during tool use.

Other cortical areas While the purpose here was to outline the insights about functions in the most relevant areas there are a variety of additional areas involved in the motor act of grasping. By using PET in human subjects Rizzolatti, Fadiga, Matelli, et al. (1996) for example could demonstrate that some areas in the temporal lobe, an area which we will allude to below in more detail, are responsive to human grasp movements as well.

1.5.3 Vision

As it was outlined above, the parietal lobe plays an important role in visuo-motor transformations. In the preceding sections we approached this region from the motor perspective. In the following section an overview about how vision integrates into this picture will be given. Firstly the path the visual signals take from the retina to the visual cortex will be outlined. Then an overview of some of the most important theories regarding the transformation of visual signals into perception and motor plans will be given.

The visual path from eye to cortex In the human visual system light is transformed into electrochemical potentials in the photoreceptor cells of the retina. Via the bipolar cells the signal is given to ganglion cells whose fibers constitute the optic nerve. The human retina consists of about 20 different types (Kolb, 2003) of these ganglion cells which also relate to different visual properties. We will focus on two particular types of ganglion cells here: the midget and the parasol cells. Those cells project to different layers of the next processing stage, the lateral geniculate nucleus (LGN) of the thalamus. While the midget cells, which have small receptive fields, project to the parvocellular layers, the parasol cells propagate the input from their large receptive fields to the magnocellular layers. These different cell types of the LGN have very different properties. Neurons in the magnocellular layers differ from those in the parvocellular layers in that they have a faster and more transient response, a higher contrast gain, larger receptive fields and an insensitivity to color (Haarmeier, 2003, p. 43). The cortical processing of the output of magno- and parvocellular layers was first believed to stay unconnected (Livingstone & Hubel, 1988). In the meantime, however, it has been shown that this is not necessarily the case (Gegenfurtner & Hawken, 1996).

From LGN the visual input is propagated to the primary and secondary visual cortices (V1 and V2) and subsequently to a variety of different visual areas. In their classic paper Felleman and van Essen (1991) have reviewed a large amount of studies

in order to trace the connections between the different visual areas of the macaque monkey and thereby have pictured the hierarchical dependencies.

Models on visual processing for action *Cortical vs subcortical vision:* As the mere knowledge about connectivities in itself only gives limited information about the workflow of a system several models have been developed in order to describe how the visual information is processed in the brain. Since most actions are visually guided this has also resulted in hypotheses about which separations and transformations are done to the visual information for the development of action plans. In the remainder of this section the according models will shortly be sketched in their chronological order and some related evidence will be discussed. The basis of this overview are the detailed account of A. D. Milner and Goodale (1995, p. 20ff) and the summary Hesse (2008, pp. 2-14) gives on this topic.

In monkey and human anatomy two distinct visual systems are found: There is a phylogenetically old route leading from the retina via the optic tectum to the pulvinar, a part of the midbrain. The other system, which is newer but heavily evolved, leads from the retina via the LGN to primary visual cortex. Due to their respective paths they can be called the *tecto-pulvinar* and the *geniculo-striate* system. Trevarthen (1968), being aware of these two systems, assigned two different functionalities to the phylogenetically new and old system: He thought of the tecto-pulvinar system being responsible for a coarse overview about the surroundings and gross navigation of the body in space (ambient vision) while the phylogenetically new, the geniculo-striate system, would carry out vision on a fine spatial scale and accordingly be responsible for more precise movements (focal vision). Schneider (1969) explained the same anatomical division with different concepts. According to this author the distinction is not about spatial scale but rather about meaning versus location. In his view the tecto-pulvinar system is responsible for delivering information about the location of an object and the geniculo-striate system extracts the information about its identity.

Divisive models of the cortex: Both Trevarthen and Schneider explained the different capabilities of the visual system on the basis of the division into the tectopulvinar and the geniculostriate system. Thus, the division was one between a subcortical and a cortical path of processing. More than a decade later Ungerleider and Mishkin (1982), however, also proposed a division within the geniculostriate system or more precisely the following higher areas of processing. They suggested that we find two streams of vision in the cortical architecture. The anatomical foundation of these streams is seen in the two neural transmission systems of the fasciculus longitudinalis superior and inferior. These fasciculi both emanate from the occipital lobe. The superior fasciculus reaches the frontal lobe by transitting the posterior parietal areas on his way. The inferior fasciculus connects the occipital with the temporal lobe. Due to their according positions with regard to Forel's axis the occipitoparietal route was labeled the *dorsal pathway* and the occipitotemporal route the *ventral pathway*. Ungerleider and Mishkin demonstrated that monkeys lesioned in the target areas of the ventral pathway—the inferotemporal cortex—had difficulties when they had to chose objects based on object-specific features like shape. They had, however, no problems chosing the right object based on its spatial relation to another object. Monkeys lesioned in the target areas of the dorsal pathway—the posterior parietal cortex—showed the reverse pattern. From these findings alongside with other evidence like the large receptive fields of neurons in inferotemporal cortex—which makes them useless for the localization of entities but useful for their identification across the whole field of vision—Ungerleider and Mishkin (1982) concluded that the dorsal pathway is used for localizing things (*where*) and the ventral pathway codes their identity (*what*).

An influential idea brought forth a few years later by Livingstone and Hubel (1987, 1988) was the mapping of the different classes of LGN cells to the two proposed streams of processing. These authors concluded from their own and the research of others conducted in monkey and human that the output from parvocellular layers of the LGN is routed to the ventral areas while the output from the

magnocellular layers goes dorsally. Although they acknowledged that some mixing might occur in higher visual areas they claimed that generally the distinction holds true and can account for findings in human perception like for example poor motion perception of isoluminant stimuli. In the meantime, however, it can be said that evidence for this claim was somewhat eroded (see for example Gegenfurtner & Hawken, 1996).

The latest model on the visual system presented here is the one by A. D. Milner and Goodale (1995). Reviewing a wealth of research conducted by themselves and others these authors proposed a re-interpretation regarding the functions of the two cortical visual pathways: According to them the ventral stream serves the purpose of generating a conscious representation of the environment surrounding us (*vision for perception*), while the dorsal stream is guiding our behavior (*vision for action*). One of the strongest supports to their claims came from a study of two different patients (Goodale et al., 1994) where a double dissociation of perception and action deficits accompanying different brain lesions was demonstrated. In this study different shapes were present and had either to be grasped with a precision grip (action task) or discriminated from each other (perception task). As a dependent measure for grasp performance Goodale et al. took the distance between the axis connecting the contact points of index finger and thumb and the gravicenter of the object. Patient D.F., who suffered from visual form agnosia following a lesion in occipitotemporal areas as a result from carbon monoxide poisoning, performed at chance in the perception task while not differing significantly from a control subject in the action task. Patient R.V., who was left with considerable damage to both parieto-occipital cortices following a stroke incident and showed the clinical picture of optic ataxia, performed considerably above chance in the discrimination task while differing from DF and the control subject in the grasp task.

This action/perception interpretation of the dorsal/ventral division has been very influential recently and has motivated a great deal of research. However, despite its popularity the data on it are inconclusive to the day. While in the meantime some

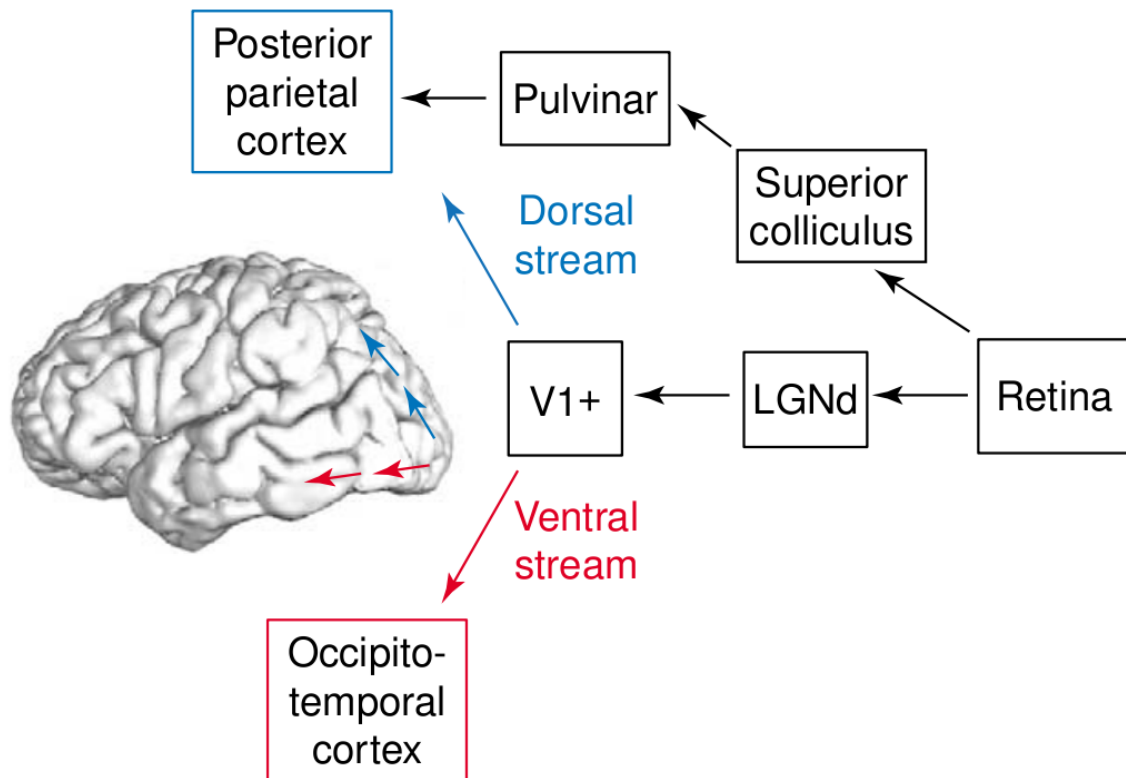


Figure 1.4: Depiction of the phylogenetically older tecto-pulvinar and the newer geniculostriate system and its subsequent subdivisions. In the tecto-pulvinar system visual information from the retina is propagated to the superior colliculus, a part of the tectum, and subsequently to the thalamic pulvinar. In the geniculo-striate system the information from the retina reaches the early visual areas, depicted here as V1+, via the dorsal lateral geniculate nucleus (LGNd). Subsequently it is splitted into the *ventral stream* and the *dorsal stream* and reaches the occipitotemporal and posterior parietal cortices respectively. The streams and their associated cortical areas supposedly carry and process different qualities of the visual information as it is outlined in the text. Reprinted from Goodale et al. (1994)

authors refer to it as the *de facto* standard model of the visual brain (e.g. Atkinson et al., 2006; Kaas & Lyon, 2007), over the last years also a notable body of evidence has accumulated which can not be brought into accordance with it. One example where evidence for the model was challenged is the predicted effect on the actions of healthy participants when grasping visual illusory displays. In the first edition of their book *The visual brain in action* A. D. Milner and Goodale (1995) quoted the results of a study of Aglioti, DeSouza, and Goodale (1995) in support for their model. These authors asked their subjects to grasp discs which constituted the inner circle of an Ebbinghaus-type illusory display. In half of the trials the two presented discs were physically of the same diameter but appeared perceptually different due to the illusion. In the other half of the trials disc diameters differed to the amount necessary for the illusion to induce the percept of identical size. Aglioti et al. (1995) reported that hand opening during grasping was influenced less by the illusion than the mere perception of disc size. These findings were interpreted as evidence for an uncoupling of ventral and dorsal streams in healthy participants as only the ventral stream is believed to code for the relative size of objects while the dorsal stream is believed to use absolute metrics. For this reason only vision-for-perception should be illusion prone but not vision-for-action. In the following years the experiment was repeated with the same and different methods several times with seemingly different results. The results and the conclusions drawn from the original Aglioti et al. (1995) study were questioned by several authors for different reasons (see Smeets & Brenner, 2006; Franz & Gegenfurtner, 2008 for reviews). As a consequence in the second edition of *The visual brain in action* A. D. Milner and Goodale (2006, p. 242) just claim that observing the proposed effect in *some* studies is enough to support the model. Franz and Gegenfurtner (2008), however, recently demonstrated that the illusion can consistently be found in grasp movements if the dependent measure is correctly adjusted to the task. The proposed interpretation of patient D.F.'s data from the study of Goodale et al. (1994) was questioned as well when Schenk (2006) published results from a pointing task with D.F. and ten control subjects.

He proposed that D.F.'s deficits are not of a mere perceptual nature but depend on the frame of reference used in the task. The authors arrived at this conclusion because D.F. was able to do a perceptual just as well as a visuomotor task, as long as objects were coded in an *egocentric* reference frame which was centered on her finger. She exhibited severe problems, however, when she had to use an *allocentric* reference frame which was centered on a cross of the visual display used (but see A. D. Milner & Goodale, 2008 for an alternative explanation of these findings).

The two-visual-systems hypothesis has inspired the research done in chapters 2 and 3 of this thesis. In the project presented in chapter 2 we tested if color is a sufficient object feature to guide our healthy participants grasp actions. As the action guiding dorsal stream is linked to the color insensitive magnocellular pathway pure color contrast should be an insufficient input for programming actions like grasping when the model of A. D. Milner and Goodale (1995) holds true. The work presented in chapter 2 has been published in the journal *Experimental Brain Research* in 2009 (see Kleinholdermann, Franz, Gegenfurtner, & Stockmeier, 2009 in the references section). In chapter 3 two patients suffering from optic ataxia were measured. Here we tested specific claims which were made on the characteristics of delayed movements in those patients. A more detailed account will be given in the introduction of the respective chapters.

1.6 Models of grasping

The aim of science is to understand the laws of nature. Apart from the mere satisfaction of the innate human curiosity this understanding gives us the means to predict and to control our environment. The scientific method consists of generating a model about phenomena and their causes, inferring testable hypotheses from the model and then gathering relevant data suited to test these hypotheses. In order to do so the observable phenomena of nature have to be formalized. Often, however,

it is difficult to decide about the right formalism for a certain class of phenomena. As it was mentioned above, in the case of movements of the upper limb, including grasping, even a complete description of how the involved joint angles change over time just gives us information about posture but tells us not much e.g. about the corresponding muscle activation patterns.

Also in the description of complex phenomena, however, in the beginning it is often useful to start out with a relatively simple description. Grasp research is certainly still in its beginning as we can consider Napier (1956) as the founder of modern research into grasping. Luckily it is also justified to simplify the approach as in grasping much less than the possible amount of complexity is realized by humans. The different postures our hands can assume make up for an impressive toolbox. Nevertheless, the number of postures actually used by us in daily life is just a small subset of all possible configurations.

In this thesis I will deal with a certain subset of grasp movements only: the precision grip grasp. This particular grasp is carried out with the thumb and another digit, mostly the index finger. It is directed towards small, relatively lightweight objects. As the basis for discussing the formal models on grasping in the following section first an overview about the normal kinematics of precision grip grasping will be given. Afterwards different models on grasping will be discussed. For this purpose we will first look at how the problem can be solved from an engineering perspective. Afterwards we will focus on the special case of grasping in humans (see also Hesse, 2008, pp. 21-22 and pp. 16-17 for a short overview on models of human grasping and an account on the kinematics of precision grip grasp movements).

1.6.1 The kinematics of the precision grip

For the description of precision grip grasp movements most of the time a much simpler formalism is chosen than joint angle space. Researchers have mostly focussed on the positions of the fingertips of the digits involved in the grip. These positions themselves can also be represented in different ways. One of these ways is to report

the timecourse of the opening between the digits—the grip component—and the position of the hand in space over time—the transport component. For historical reasons most of the findings are reported using this frame of reference.

In a pioneering series of experiments (Jeannerod, 1984, 1986) laid much of the foundation for the contemporary research on grasping. He found out how the digits move when they approach the target of a grasp: We see a profile of digit opening and closing where a maximum opening of the digits is reached when more than half of the total movement time has passed. This maximum grip aperture (MGA) linearly scales to the final grip aperture when the digits enclose the object at the intended grasp positions. These findings are very stable and have often been replicated (see Smeets & Brenner, 1999 for a review). A model on precision grip grasping thus should be able to generate an aperture profile with these features.

The transport of the hand towards the grasp target is also called the reach component. Jeannerod described the reach component as having a bell-shaped velocity pattern. This means that there is a non-linear acceleration phase followed by a more or less prominent plateau which in turn is followed by a non-linear deceleration phase. Also the shape of this velocity profile should be captured by a plausible model on grasping.

There are a lot more parameters which can be measured in grasp movements. Important features are for example the reaction time (RT), the total movement time (MT) as well as the endpoint and the trajectory variability. All of these parameters may be sensitive to changes in the task and can be used to experimentally arrive at conclusions about the underlying planning strategies of the CNS. These parameters, however, are not uniquely found in grasp movements but are shared with other movement classes like for example pointing movements. The aperture profile in contrast is exclusively found in grasp movements and model approaches have mostly focused on it and the speed profile which is necessary to predict the movement path. More details on the different dependent measures will be given in the introduction of chapter 2.

There is one more parameter which is necessary for a complete description of grasping but will be mostly ignored in the remainder of this thesis: The force applied to the digits in the final grasp posture. There has been extensive research done on this topic by Johansson (1996, 1998) who found that grip force is elegantly adjusted to the task at hand by the motor system.

1.6.2 Grasping as an engineering problem

Starting with the industrial revolution and the mechanical loom more and more tasks formerly accomplished by human hands have been assigned to machines. Therefore the effectors of these machines somehow had to mimick actions of the human hand. Over time those machines have been developed further and further. Nowadays automatized grippers are available in a variety of shapes, optimized for a variety of different tasks.

In most automatized applications the problem of grasping a certain workpiece can easily be solved because the part comes from a known set of objects. In this case the question is merely how to get from the current posture to the desired but already known goal posture. Since the speed profile can be chosen more or less arbitrarily in robots the problem is relatively trivial.

The more interesting problem must be solved in cases where the set of possible objects is unknown. This is for example important for systems in an unknown environment where online control is not possible. An example for this is cosmonautics where a space probe is required to pick up e.g. rock cuttings whose shapes are unknown. In this case transmission times of a control signal are far too long for online control of the gripper. Obviously this is also the kind of problem our motor system is confronted with since there are myriads of different objects of arbitrary shapes but we are nevertheless able to pick up nearly all of them. In this kind of problem the goal posture does not come from a fixed set but must first be found, generally by using visual information about the object. Although considerably harder to tackle, this problem has also technically been solved with different approaches based for ex-

ample on object geometry (cf. Nguyen, 1986; Blake, 1995) or visual features of the object (Saxena, Driemeyer, & Ng, 2008). For robot grippers the problem is mainly to find a force-closure stable configuration of the effectors (see figure 1.5 for an example). Nguyen (1986) shows how points satisfying this condition can be calculated in the 2D case on the basis of an objects contour. In short, the contact points of the grippers must be chosen in a way that a line connecting them lies inside of two friction cones. The width of these friction cones depends on the surface properties of gripper and object. The approach can easily be extended to the 3D case and transferred to the grip of human digits. This approach will be an integral part of the model on grasp point selection presented in chapter 4.

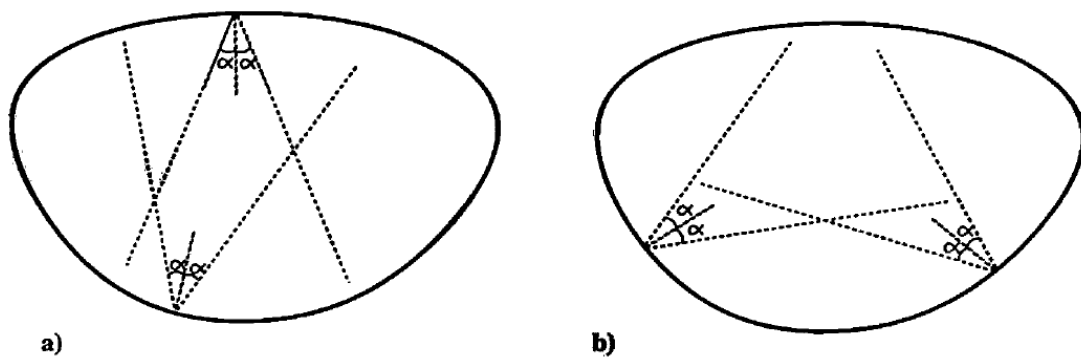


Figure 1.5: Two digit grasp configuration. The dashed lines indicate friction cones which emerge from the two grasp points at the circumference of the object. a) A force closure configuration. Each contact point lies within the friction cone of the other. b) No force closure. Applying force to the points in this case will generally result in slip of the digits or a movement of the object. Figure reprinted from Blake (1992).

1.6.3 Models of human grasping

Modelling human grasp movements is different from modelling robot movements with respect to several facets. An important difference is that reverse engineering must be applied to the problem: We can observe how the solution works but we want to know how it is implemented in the available machinery. After observing hu-

man grasp behavior and tracking it with a camera Jeannerod (1984) introduced the abovementioned influential division of the movement into a transport and a grasp component, an idea which was later seized and built upon by many other authors. Jeannerod himself has circumstantiated this view with work on patients where he for example discovered that the grip component of a movement can selectively be impaired while reaching remains intact (Jeannerod, Decety, & Michel, 1994). Furthermore he claimed that we see this distinction clearly in children who first develop the ability of reaching and only later arrive at a stage of fine motor control where they can do proper grip adjustment too (Jeannerod, 1994). This two-components view of grasping has inspired much research and was adapted and refined by other authors. Marteniuk, Leavitt, MacKenzie, and Athenes (1990) for example made suggestions about a coupling mechanism between the transport and the grip component and suggested that it may be task dependent.

Bootsma, Marteniuk, MacKenzie, and Zaal (1994) built upon the distinction between grasp and transport component introduced by Jeannerod. They added to his views by proposing that also in grasping Fitt's law (Fitts, 1954) imposes a constraint on movement time. Their proposition led to the reconciliation of earlier data (Marteniuk et al., 1990) where a dependency between object size (grasp component) and movement time (transport component) has been found which was inconsistent with Jeannerod's proposal of independent channels. From their dataset of grasps to different object sizes and widths Bootsma et al. (1994) concluded that wider objects impose less accuracy constraints on the transport component which in turn allows for a more speeded movement. This speeded movement, however, leads to more variability in the direction of object approach which in turn is compensated with a larger MGA in the timecourse of the grasp component. Their results thus show how principally independent mechanisms may generate interdependencies on the behavioral level.

Hoff and Arbib (1993) presented a quantitative model of reaching which generates movement trajectories based on the minimum jerk principle. This principle,

introduced by Flash and Hogan (1985), states that arm movements are planned in a way that jerk, the time derivative of acceleration, is minimized. This is a biologically plausible mechanism as it reduces strain on muscles, tendons and joints. The model of Hoff and Arbib (1993) just as the one of Bootsma et al. retains the distinction between grasp and transport component. It is a kinematic model which captures the position and velocity of the hand at a certain point in time during the movement. It proposes a control mechanism which monitors the current position, the goal position and the remaining time of movement. The authors put a special emphasis on the model's ability to handle perturbations of either target or hand position during movement execution. A delayed feedback mechanism for sensory feedback enables the tracking of target and hand location. Hoff and Arbib (1993) circumstantiate their model with copious comparisons of modeled and empirical data of perturbed and unperturbed movements. As the hand opening, or aperture, is modeled separately from the transport component the timing of the MGA somehow has to be coupled to movement time. This is done with a fixed timing value, the *enclose time* (ET) which is a constant for a certain task.

The problem of coupling the timing of MGA to the transport component subsequently was also solved in a neat way by Mon-Williams et al. (2001). These authors proposed that the ratio between maximum and final aperture of a grip equals the ratio of opening and closing time of the digits respectively. Using this approach one more constant can be eliminated from a potential grasp model based on the transport/grasp component approach.

The model of Smeets and Brenner (1999) used a markedly different approach from the models outlined above. Their model treats precision grip grasping as a special case of digit movement or pointing. Precision grip grasping in this view is seen as pointing with two fingers towards the final grasp points on the object surface. In order to mimick the empirically measured velocity profile of human movements Smeets and Brenner (1999) also draw on the earlier work of Flash and Hogan (1985) by using a minimum jerk approach of trajectory planning. Based on this principle

the trajectory for the participating digits is calculated independently. Apart from some rather trivial constraints, like e.g. a fixed movement time, the model has only one free parameter. This parameter is called *approach parameter* and determines the extent to which the trajectory is curved. If we consider a two-digit movement thus the approach parameter determines the aperture profile of the opening between the digits during the movement. By reviewing data of more than 30 studies Smeets and Brenner (1999) demonstrated that their model is in good accordance with empirical data. Later on also direct tests of the model (Smeets, Brenner, & Biegstraaten, 2002; Smeets, Glover, & Brenner, 2003; Kleinholdermann, Brenner, Franz, & Smeets, 2007) could demonstrate a good accordance between model predictions and data. A downside of the model of Smeets and Brenner (1999) is that it does not fit as well to our current knowledge about the functional organization of grasp and reach regions in the neocortex. As has been mentioned before (section 1.5.2) there may be different cortical regions controlling reach and grasp separately. Furthermore recently (Smeets, Brenner, & Martin, 2009) the authors themselves have presented evidence suggesting that the model only works properly in the 2D case and has difficulties to capture human movements correctly on the dimension of height. Taken into account its simplicity, however, it still shows an impressive performance. Figure 1.6 shows how trajectories of the fingers are calculated according to this model.

The model of Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, and Engelbrecht (1995) and its later modification (Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001) are the last models to be presented here. This model is an impressive piece of scientific work as it is principally not limited to grasp or point movements but can cover all possible classes of actions. The model is based on the very general idea, that the actor aims for acquiring a certain posture, which is a set of joint angles, and starts from an initial posture. It is assumed that complete representations of postures are stored somewhere in the nervous system. In the first version of the model (Rosenbaum et al., 1995) the desired posture is chosen by considering two kinds of penalty values. One is the penalty for deviating from the desired contact

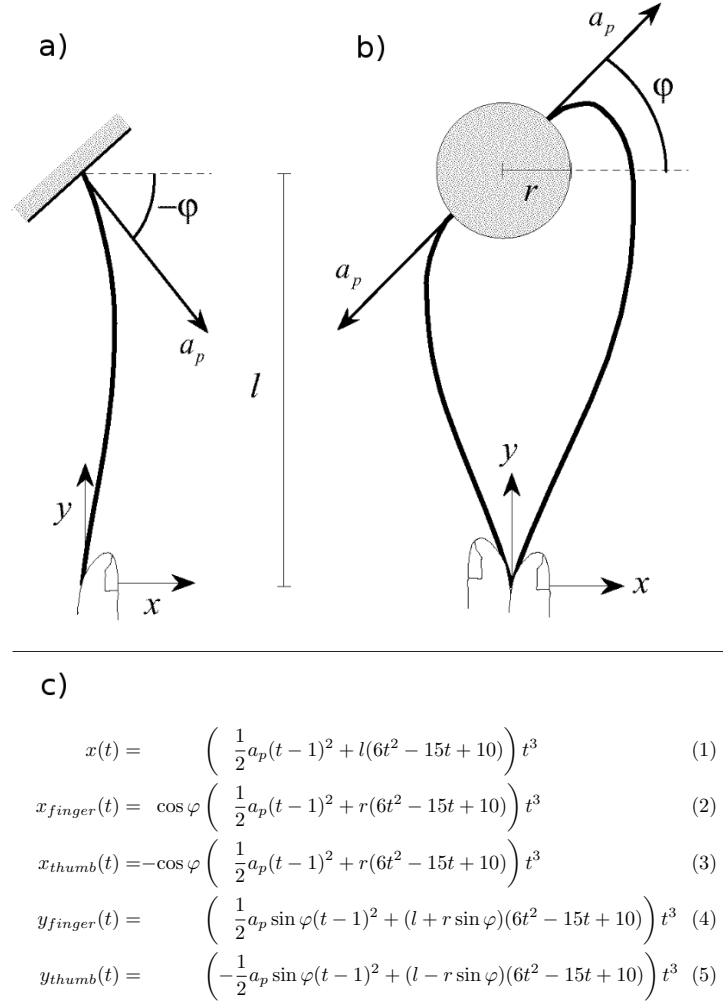


Figure 1.6: Illustration of the Smeets and Brenner (1999) model on grasping. a) Pointing movement with a single digit. Note that in the end of the movement the digit tends to approach the surface perpendicularly. The curvature of the trajectory depends on the approach parameter (a_p). The angle φ determines the direction of approach in an object independent external coordinate system (x, y -system). b) Grasping movement consisting of two combined pointing movements of index finger and thumb. c) Formal model for trajectory generation according to the model. (1) general formula for a minimum-jerk trajectory with t being normalized time and l being the distance covered by the movement. (2)–(5) Adaptation to the case of grasping a disc as it is depicted in b). Here l is the distance to the center of the disc and r the radius of the disc. Adapted from Smeets and Brenner (1999)

point. The other is a penalty value which is summed for every joint involved in the movement. This value increases with larger joint displacement and longer movement time for the joint necessary to arrive at the desired posture. The final goal posture is chosen by using an average across all possible goal postures inversely weighted with their associated costs. Realization of this goal posture is then attained by smooth movements in the joints which are modeled by means of a bell-shaped velocity profile. A neat feature of this model was the introduction of an “expense factor” for every joint which penalizes movements in that joint independently from the other joints. By this mean it is possible, for example, to model movements involving injured joints in patients. This feature is not found in any of the other models. The model can also account for the *end-state comfort effect* (Rosenbaum et al., 1990). This is the empirical finding that actors transitorily accept uncomfortable postures if in the end they arrive at a comfortable posture. Later Rosenbaum et al. (2001) modified the model with respect to some aspects. Rather than considering only two costs now a whole list of objectives, a *constraint hierarchy*, was taken into account. Still the members of this hierarchy can differently be weighted according to the task at hand. The weighted average rule was replaced by an algorithm which makes a initial guess and a subsequent time-limited refinement. Another improvement consisted of the implementation of a mechanism for obstacle avoidance. Rosenbaum et al. (2001) presented a neat solution to this problem. In their approach the initially planned movement trajectory stays untouched. Rather, a second movement is added to it which goes from the startpoint away from the obstacle and back to the start point. Both movements are carried out simultaneously. Therefore the end-position of the movement is not changed but the trajectory is modified in such a way that the obstacle is avoided. The assumptions the posture model makes are quite strong and it has a lot of free parameters. Smeets and Brenner (2002) did a direct comparison of this model with their own model (Smeets & Brenner, 1999) and found that both models perform about equally well. Since the posture model has a much higher complexity thus the model of Smeets and Brenner (1999) could be seen as being

the more elegant solution to the problem. Furthermore some aspects of the posture model have already been acknowledged to be wrong (Rosenbaum et al., 2009), as for example human movements seem not to follow minimum-jerk trajectories of joint angle change as it is assumed. The posture model can nevertheless be considered as being a very valuable approach. Firstly it has an unmatched generality as it can be applied to all kinds of movements. Secondly it models human movements in a physiologically plausible way while the model of Smeets and Brenner (1999) blinds out much of the underlying human anatomy and thus, for example, can predict movement paths which are impossible to perform by humans.

Although the models presented above all use different approaches to generate movements to desired goal locations they have one thing in common: All of them lack a mechanism which can determine where the desired locations are. This gap in current model approaches of human hand movements has motivated the research presented in chapter 4. In the work presented there techniques from robotic grasping are combined with choice mechanisms which are physiologically plausible for human graspers. Based on this synergy a strategy for finding goal points in human precision grip grasp movements will be presented.

Chapter 2

Grasping isoluminant stimuli

Abstract

We used a virtual reality setup to let participants grasp discs which differed in luminance, chromaticity and size. Current theories on perception and action propose a division of labor in the brain into a color proficient perception pathway and a less color-capable action pathway. In this study we addressed the question whether isoluminant stimuli which provide only a chromatic but no luminance contrast for action planning are harder to grasp than stimuli providing luminance contrast or both kinds of contrast. We found that grasps of isoluminant stimuli had a slightly steeper slope relating the maximum grip aperture to disc size but all other measures of grip quality were unaffected. Overall our results do not support the view that isoluminance of stimulus and background impedes the planning of a grasping movement.

2.1 Introduction

Current theories on vision divide the visual system into two major pathways (Ungerleider & Mishkin, 1982; A. D. Milner & Goodale, 1995). One of these models distinguishes a ventral pathway which is mainly concerned with conscious perception from a dorsal pathway which is responsible for the development of action plans (Goodale & Milner, 1992; A. D. Milner & Goodale, 1995). Corresponding to the different purposes both pathways are supposed to serve, they receive different parts of the available visual information. The ventral system, responsible for delivering a perseverative percept of objects and their spatial relation to each other, has a low temporal but high spatial resolution and a high sensitivity to chromaticity of visual stimuli. This has been shown in numerous studies in monkeys (Zeki, 1973, 1978; Komatsu, Ideura, Kaji, & Yamane, 1992; Takechi et al., 1997; Huxlin, Saunders, Marchionini, Pham, & Merigan, 2000) and humans (Meadows, 1974; Damasio, Yamada, Damasio, Corbett, & McKee, 1980; Lueck et al., 1989; Zeki, 1990; Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; Beauchamp, Haxby, Rosen, & DeYoe, 2000; Wade, Brewer, Rieger, & Wandell, 2002). This can be understood on the basis of the response characteristics of the cells in area V4 which constitute the main source of input for this visual subsystem (Zeki, 1980, 1983; Heywood, Gadotti, & Cowey, 1992; Felleman & van Essen, 1991). The dorsal system on the other hand, receives its main input from area MT which has only a small number of color sensitive neurons (Saito, Tanaka, Isono, Yasuda, & Mikami, 1989; Gegenfurtner et al., 1994) and whose cells mainly respond to motion (Dubner & Zeki, 1971; Maunsell & van Essen, 1983; Maunsell, Nealey, & DePriest, 1990; Born & Bradley, 2005). This leads to a lower sensitivity for color and fine spatial resolution compared to the ventral system. Instead temporal resolution and thus movement sensitivity are better in the dorsal than the ventral pathway.

Since the ventral system is proposed to be the major, if not the exclusive source of our conscious percept of the world (Goodale & Milner, 1992; A. D. Milner &

Goodale, 1995) it has been a challenge for researchers to come up with experiments where conscious perception and motor planning are at odds. These experiments rely for example on the sensitivity for certain visual illusions, which are thought to not influence motor plans, while being perfectly visible to an observer (e.g. Aglioti et al., 1995 but see: Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Franz, 2001; Franz, Hesse, & Kollath, 2009). Another branch of research has dealt with neurological patients showing selective deficits assumed to result from a confined lesion to one or the other pathway (c.f., A. D. Milner & Goodale, 1995; Himmelbach & Karnath, 2005). Currently also the effects of stimulating regions associated with one or the other pathway by means of rTMS are investigated (e.g. Schenk, Ellison, Rice, & Milner, 2005).

In this study we were interested whether the chromaticity of objects is a sufficient feature to establish motor plans for grasp movements. Because only a small fraction of MT neurons respond to chromatic information one could suppose that movement planning is impaired when a chromatic difference is all which distinguishes the target of a movement from its background. In this case the dorsal system either somehow has to deal with the limited information it possesses, which should lead to an impaired movement, or it has to draw upon the information available in the ventral pathway which should delay movement execution. The latter was shown for example by Pisella, Arzi, and Rossetti (1998) who found a longer latency in a perturbed pointing task when color instead of position was the stimulus attribute (but see Brenner & Smeets, 2004). If we would find an impaired or delayed movement towards a perceptually clearly visible target this would be an argument in favor of two distinct channels for movement planning and conscious object perception. If on the other hand chromatic information is perfectly sufficient to plan and execute the movement in a completely normal fashion this would suggest a more holistic view of the perception/action system or at least the notion that crosstalk between the systems is more profound than is commonly thought. This is also what Gentilucci, Benuzzi, Bertolani, and Gangitano (2001) suggested when they found a color ef-

fect on target size estimates. In their study they showed that red targets are over- and green targets underestimated. This, however, was not only true in a manual size estimation task but also observed in grasping movements, pointing to a general process underlying both, perception and action.

In this study we therefore assessed the quality of grasp movements towards stimuli which differed in luminance and chromaticity. Our special interest was on those stimuli which only had a chromatic contrast to the background while their luminance was equal to it (isoluminant stimuli). We wanted to know if those stimuli, because they are solely defined by a property which is not an optimal input for the dorsal stream, impose a challenge to the motor system or are grasped just as stimuli providing luminance contrast or chromatic and luminance contrast together.

In order to assess the quality of a grip we used several measures which have been shown to be related to the availability of object information for movement planning. As the main measure of interest we calculated the maximum grip aperture (MGA). Since the well-known studies of Jeannerod (1984, 1986) the MGA has proven to be a reliable indicator of size information availability in the visuo-motor system. Usually one finds a linear relationship between object size and MGA with a slope coefficient of about .82 (average slope value in the Smeets & Brenner, 1999 review of 35 studies). When the amount of visual information about the object is reduced the normal reaction of participants is a general increase of MGA. This was found in cases where the object was retinally sampled on a coarser scale because it was presented in the periphery of the visual field (Brown, Halpert, & Goodale, 2005; Schlicht & Schrater, 2007). It was also observed when sight onto the object was removed before movement initiation (Wing, Turton, & Fraser, 1986; Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Franz et al., 2009; Hesse & Franz, 2009) or during the movement (Jakobson & Goodale, 1991; Franz et al., 2009; Hesse & Franz, 2009) such that the movement had to be executed relying on memorized information which is subject to a rather rapid decay (Hesse & Franz, 2009).

In contrast to the clear effect of reducing the amount of visual information on

the absolute size of MGA the linear scaling of MGA to object size usually remains surprisingly unaffected. In the studies of Jakobson and Goodale (1991), Brown et al. (2005) and Franz et al. (2009) scaling remained the same for all conditions which changed the amount of visual information as can be inferred from missing interactions of those conditions with the factor object size. Hesse and Franz (2009) even addressed the issue directly by statistically testing the slope of the scaling function and also found no effect of viewing condition. A significant interaction between viewing condition and object size however was found in the study of Berthier et al. (1996). Here the authors used a full vision condition, a reduced vision condition where the target object was glowing in an otherwise dark room and a condition without vision where subjects blindly grasped towards an object which was previewed before the trial but whose position was only indicated by a sound during the actual grasp trial. In this study the slope got shallower for the conditions where visual information is reduced. This result though should be interpreted cautiously since the main source of the interaction effect seems to originate from two objects which were unusually small (4 mm and 9 mm) compared to sizes used in the abovementioned studies (ranging between 20 mm and 50 mm) which are more representative for the literature on precision grip grasping.

Another important indicator of grip quality is the time of MGA occurrence. Smeets and Brenner (1999) report in their review that MGA most often can be found in the last third of the movement. They also show that the timing of MGA depends on target size (see also Schettino, Adamovich, & Poizner, 2003). Furthermore Weir, MacKenzie, Marteniuk, and Carboe (1991) discovered that the relative time of MGA is earlier for objects with more slippery surfaces. These findings indicate that grasps which are more difficult may have an earlier occurrence of MGA. We would therefore expect that a target which is less visible to the motor system would also elicit such a change in MGA timing.

There are two more temporal markers that have been shown to be sensitive to diminished information about the target object of a grasp movement: the movement

time (MT), which gets longer (Schettino et al., 2003), and the reaction time (RT) from trial onset to start of the grip (see for example Mon-Williams et al., 2001). Both measures should be prolonged if the motor system is forced to rely on degraded or delayed information.

As the last indicator of grip quality we assessed the variance of the trajectory. We hypothesized that this variance should increase in conditions with less availability of object information to the dorsal stream.

In order to compare possible effects occurring in the motor domain with the perceptual domain we also subjected our participants to a perceptual task. Here we asked them to perform size estimates of our stimuli.

2.2 Methods

2.2.1 Participants

We measured 10 participants on three occasions. All participants were right handed (Edinburgh Inventory, Oldfield, 1971) without color deficiencies (Ishihara, 1962) and naïve to the purpose of the experiment. The age average of the sample was 28 years. Half of the participants were female. For their participation participants were rewarded with eight euro per hour.

2.2.2 Stimuli

Our stimuli were discs of three different diameters (30, 35, 40 mm) and 13 different colors. The discs were displayed on a computer monitor and seen via a mirror (see the description of the setup below). The set embodied 10 discs of green chromaticity (CIE: $x=.281$, $y=.583$). One of these discs was isoluminant with the background according to the CIE standard observer (photometric isoluminance). In order to deal with the natural variability in individual isoluminance between observers another green disc was made individually isoluminant for the participant by means of hete-

achromatic flicker-photometry (subjective isoluminance). The luminance contrast of this disc with the background therefore varied in a range between +1.8 % and +10.9 % ($\bar{x} = 6.5$ %, $\sigma = 2.8$ %). The luminance of the remaining eight green discs was varied around photometric isoluminance (-8, -4, -2, -1, +1, +2, +4, +8 percent of luminance contrast with the background) in order to assess effects which may occur around the point of isoluminance.

In addition we presented three achromatic discs, two above (+3 and +43 percent) and one below (-12 percent) the luminance of the background which was at $25 \frac{cd}{m^2}$.

In the grasp task aluminium discs of 5 mm height matched up with the perceived position and diameter of the projected discs. In the perceptual task the standard disc which was used as a comparison was always achromatic and bright (143 % of background luminance).

2.2.3 Setup

Participants were seated in front of a virtual-reality setup which consisted of a monitor/mirror projection system and the table where our target discs for grasping were placed upon (fig. 2.1). The monitor image was projected onto the mirror and produced a virtual image of the display. Distances and angles between monitor, mirror and the table under the mirror were chosen such that the virtual image when looked at was perceived being at the height of the table surface. When a stimulus was displayed on the monitor participants who sat in front of the mirror therefore perceived the stimulus to lie on the table in front of them. In our grasp task we positioned the real target disc at exactly the position where the virtual disc image was congruent with it. The perceived distance of the stimuli was then at about 50 cm from the participants eye.

Grasp movements were recorded with an Optotrak 3020 infrared tracking system at a sampling rate of 100 Hz. Three infrared markers were attached to the nails of the index finger and thumb. Using three markers per digit allowed for measuring the touch points on the participants pad surfaces in relation to those markers. At

the same time the pad surfaces stayed free for the grip, allowing full tactile feedback.

The perceptual size estimates and the heterochromatic flicker isoluminance values were collected on the same setup with a computer mouse.

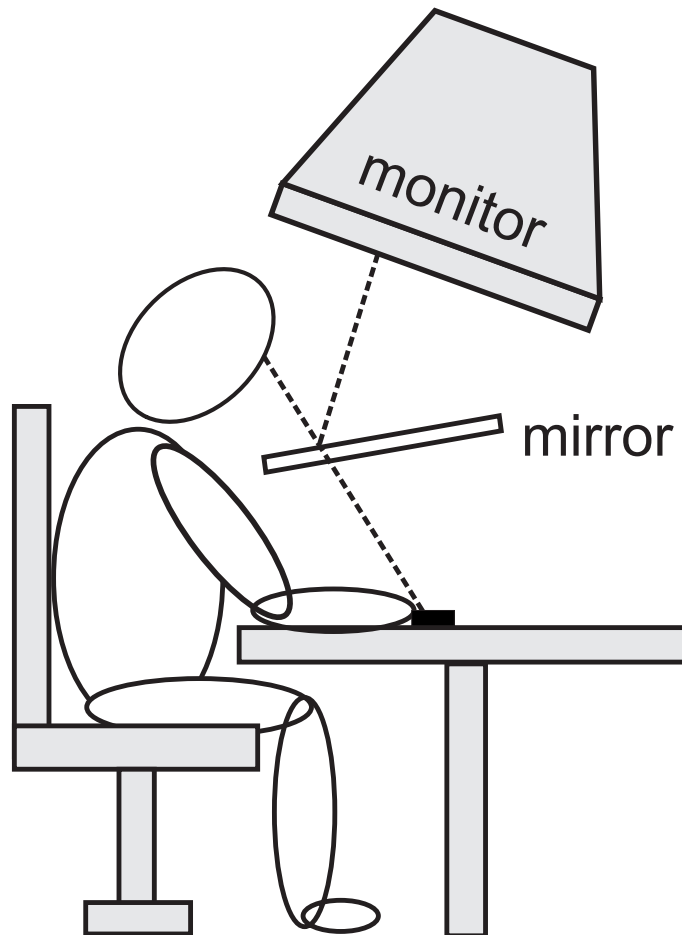


Figure 2.1: Experimental setup. Participants looked into a mirror which reflected the image of the monitor. Distances and angles were chosen in a way that the perceived surface was at the height of the table onto which discs in the grasp task were placed. Reprinted from Hesse (2008), p. 82, fig 4.1a

2.2.4 Procedure

In the first experimental session we determined the individual point of isoluminance for the participant by means of flicker-photometry (c.f. Kaiser & Boynton, 1996):

A green target disc was flickered with a frequency of 15 Hz on a background of the same gray as was used later in the experiment. Participants adjusted the luminance of the disc from a random start point until the perception of flicker was minimized or vanished totally. The average luminance value of 15 trials (three disc sizes à five trials) was used to determine the subjective point of isoluminance.

For measuring the grasp movements participants sat in front of the mirror setup and looked at the virtual surface produced by monitor and mirror. Prior to each trial the experimenter placed the aluminium disc which corresponded to the presented virtual disc onto a small plastic pin which served as a mount for the disc. The trial started as soon as the image of the virtual disc was projected onto the gray background. Participants then had four seconds time to grasp the disc with a precision grip of index finger and thumb and transport it to a goal area. After the grasp participants moved the fingers back to the starting point, a small pin affixed to the experimental table, and the next trial was prepared. All movements were made under open loop conditions that is no visual feedback of hand or finger position was provided because the digits were obscured by the mirror. The projected target disc image was visible from the beginning of the trial until the real disc was grasped and lifted 20 mm. In each of the three experimental sessions participants grasped every size/color combination three times which makes 117 grasps per session and 351 grasp trials for every participant in total.

In the perceptual task participants had to match the radius of the target disc to a standard disc of either 30, 35 or 40 mm diameter. The initial diameter was randomly chosen between 25 and 45 mm in steps of 1 mm. The target appeared either to the left or to the right of the standard disc. The diameter adjustment was made in 0.2 mm steps by hitting the left and right buttons of a computer mouse. Participants could take as much time as they wanted for the adjustment. When the adjustment was finished participants hit the center mouse button and the next target/standard pair appeared. In each session participants adjusted every size/color combination two times which resulted in 78 trials per session and 234

trials total per participant across all three sessions.

In each experimental session there was one block for the perception task and one for grasping. The order of blocks was reversed in the next session and counterbalanced between participants.

2.3 Results

2.3.1 Grasp parameters

Figure 2.2 shows the mean MGA for the different disc colors and disc sizes. While there was a clear effect of disc size on MGA the effect of disc color was nonsignificant as was the interaction. Thus the absolute size of MGA was not affected by changing the color of stimuli.

The slopes of MGA as a function of disc size in the different color conditions are shown in figure 2.3. We calculated a least square linear regression of MGA on disc size for each participant and computed a repeated measures ANOVA of the slope coefficients. There was a main effect of disc color (see table 2.1 for all F-values). Fisher LSD adjusted post-hoc tests revealed significant different slopes between the subjective isoluminant condition and all other color conditions (all $p < .05$) except for the green discs with -4 and +8 percent deviance from background luminance. The overall slope of MGA on disc size across all participants and color conditions was 0.77.

All temporal measures of the grip were unaffected by variations of disc size and color as can be seen in table 2.1. Mean RT was at 394 ms ($\sigma = 133$ ms), mean MT at 788 ms ($\sigma = 255$ ms) and mean time of MGA at 449 ms ($\sigma = 137$ ms).

The analysis of our last movement-quality measure, the movement variance, also showed no effect of disc size or color on the movement.

Table 2.1: Results of Repeated Measure ANOVAs

Measure	Mean	SE	Factor	df_1	df_2	F	p
MGA	65mm	2.875	Size	2	18	99	<.001***
			Color	12	108	0.96	.49
			Interaction	24	216	1.2	.24
Slope of MGA ^a	0.766	0.069	Size	–	–	–	–
			Color	12	108	1.9	.038*
			Interaction	–	–	–	–
Time of MGA	449ms	31.448	Size	2	18	1.6	.23
			Color	12	108	0.79	.66
			Interaction	24	216	1.1	.35
MT	788ms	51.497	Size	2	18	2.9	.079
			Color	12	108	1	.41
			Interaction	24	216	1.3	.15
RT	394ms	18.717	Size	2	18	2.1	.15
			Color	12	108	1.4	.17
			Interaction	24	216	0.95	.54
Finger variance	150mm ²	14.149	Size	2	18	0.68	.52
			Color	12	108	0.65	.79
			Interaction	24	216	1	.45
Thumb variance	138mm ²	12.963	Size	2	18	0.49	.62
			Color	12	108	0.67	.78
			Interaction	24	216	1	.43
Perceptual size estimates	34mm	0.278	Size	2	18	5847	<.001***
			Color	12	108	15	<.001***
			Interaction	24	216	0.55	.96
Perc. size est. slopes ^a	0.989	0.012	Size	–	–	–	–
			Color	12	108	0.6	.84
			Interaction	–	–	–	–

^aBecause the slopes are calculated across all sizes there is no factor size for them.

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

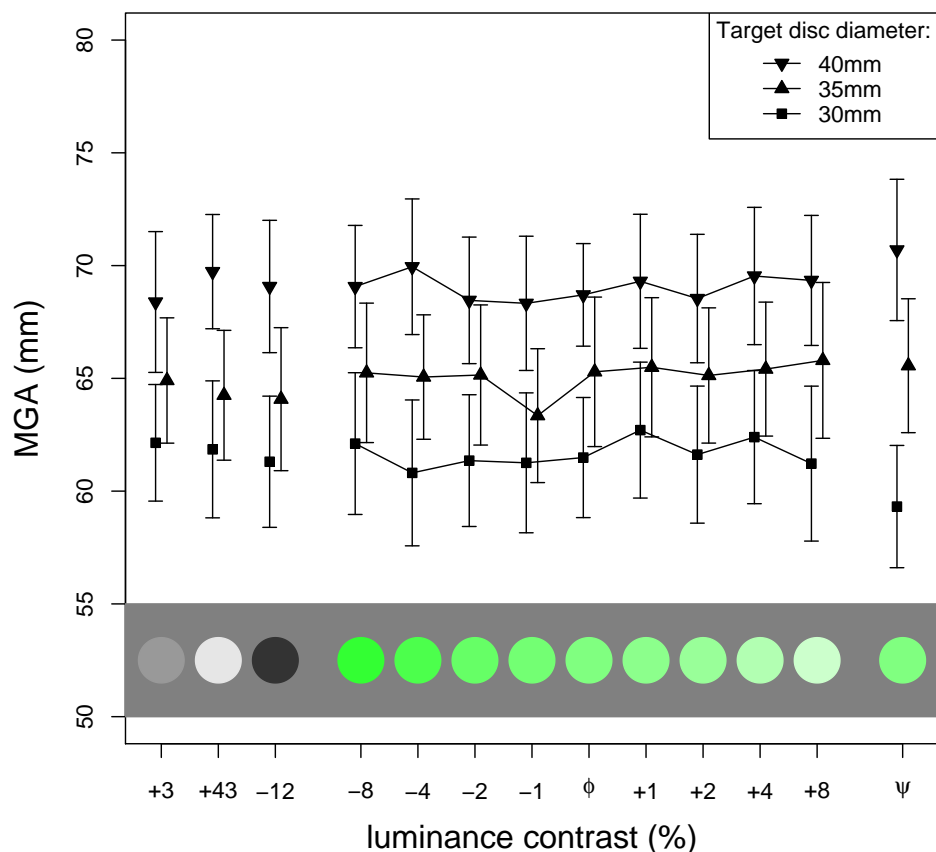


Figure 2.2: Mean MGA for different disc sizes and color conditions. Values on the abscissa depict the luminance contrast with the background in percent. Φ : photometric isoluminance. Ψ : subjective isoluminance. Errorbars are ± 1 standard error of the mean (between subjects).

2.3.2 Perceptual size estimates

The data of perceptual size estimates are shown in figures 2.4 and 2.5. The ANOVA revealed significant main effects for disc size as well as disc color. The interaction was insignificant. Several Bonferroni adjusted posthoc-tests were significant at $p < .001$. The complete results can be found in table 2.2. Significant comparisons are only found for the achromatic stimuli. Especially the achromatic stimuli with -12 and

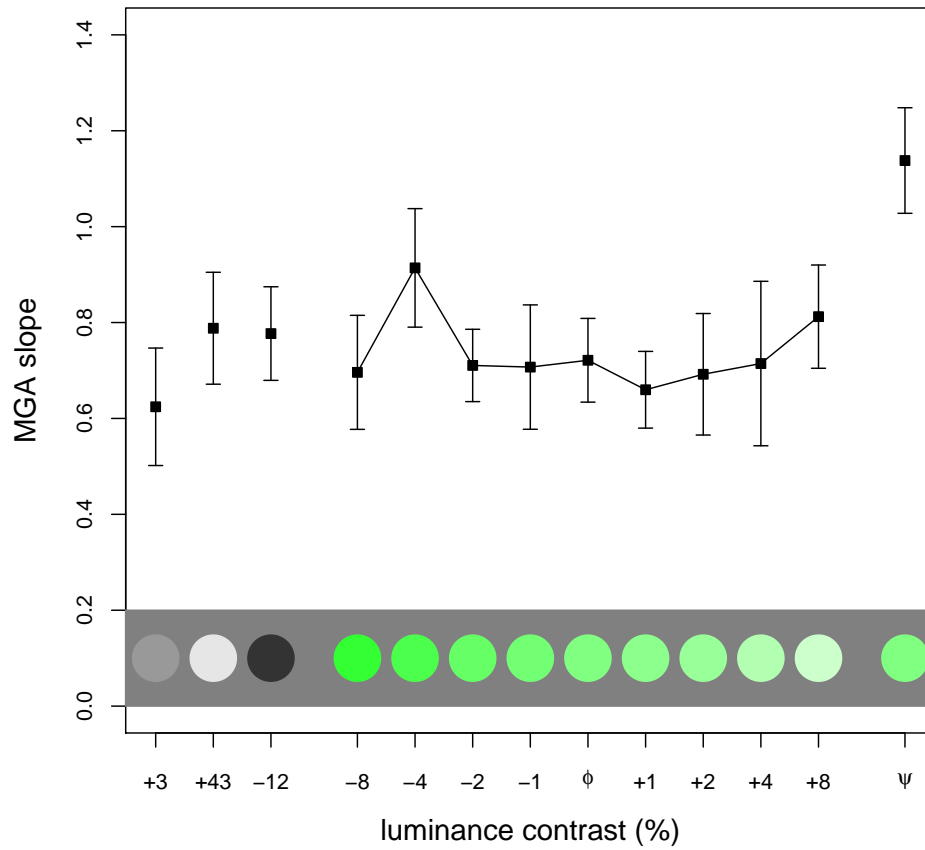


Figure 2.3: Mean slope of MGA in the different color conditions. Values on the abscissa depict the luminance contrast with the background in percent. Φ : photometric isoluminance. Ψ : subjective isoluminance. Errorbars are ± 1 standard error of the mean (between subjects).

+3 percent of background luminance were underestimated compared to the other stimuli.

Table 2.2: Perception Posthoc Test p -Values. Row and Column Numbering Indicates the Luminance Contrast with the Background in Percent. Φ : Isoluminance for the CIE Standard Observer. Ψ : Subjective Isoluminance.

	+3	+43	-12	-8	-4	-2	-1	ϕ	+1	+2	+4	+8
+43	< .001***	-	-	-	-	-	-	-	-	-	-	-
-12	.826	< .001***	-	-	-	-	-	-	-	-	-	-
-8	.002	.010	< .001***	-	-	-	-	-	-	-	-	-
-4	.003	.008	< .001***	.892	-	-	-	-	-	-	-	-
-2	.001	.048	< .001***	.828	.869	-	-	-	-	-	-	-
-1	.004	.109	.001	.582	.476	.525	-	-	-	-	-	-
ϕ	.002	.001	< .001***	.925	.859	.807	.696	-	-	-	-	-
+1	.006	.059	.003	.625	.669	.590	.438	.605	-	-	-	-
+2	.003	.009	.001	.722	.832	.966	.527	.634	.751	-	-	-
+4	< .001***	.107	< .001***	.088	.088	.103	.357	.044	.159	.015	-	-
+8	.001	.193	< .001***	.017	.029	.056	.191	.052	.056	.047	.762	-
ψ	< .001***	.501	< .001***	.056	.036	.033	.122	.033	.027	.022	.345	.544

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$, Bonferroni adjusted

An ANOVA which was computed across the individual slopes of the perceptual size estimate as a function of disc size did not reveal any influence of stimulus color (see table 2.1 and figure 2.5).

2.4 Discussion

We examined the influence of color information on the quality of grasp movements. We found that the absolute value of MGA, a measure which has proven to be sensitive to the availability of visual information in the visuo-motor system, is not influenced by changing the color of grasp targets. This is also true if the target is isoluminant with the background. For the perceptually isoluminant targets, the ones for which the point of isoluminance was determined with flicker photometry, the slope of the MGA related to target size was significantly higher than for most other targets. This finding might hint to a different processing of these stimuli when the

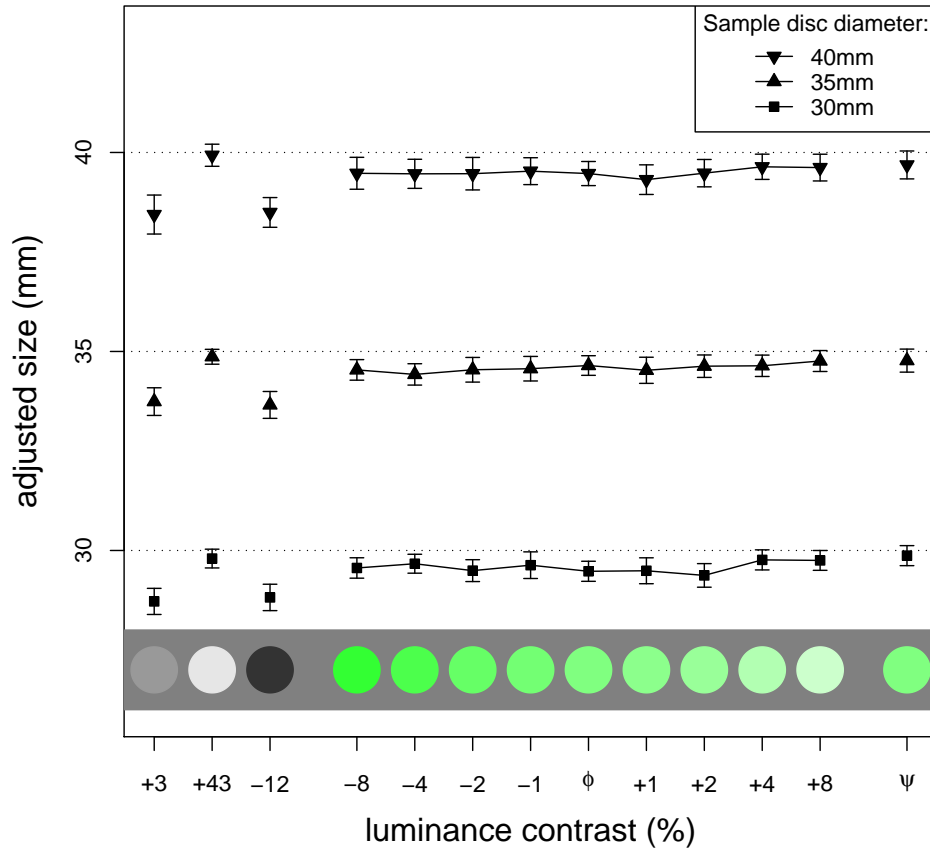


Figure 2.4: Estimated disc size as a function of disc color for different disc sizes. Values on the abscissa depict the luminance contrast with the background in percent. Φ : photometric isoluminance. Ψ : subjective isoluminance. Errorbars are ± 1 standard error of the mean (between subjects).

movement plan is made by the brain. The result though is not in accordance with what one would expect if there were less size information about the target available in the motor system. In this case the slope of MGA should rather decrease than increase with a concomitant increase of the average MGA: participants are unsure how large the object is and produce the same very wide opening of their digits in each trial to cover all possible object sizes. This is also what Berthier et al. (1996)

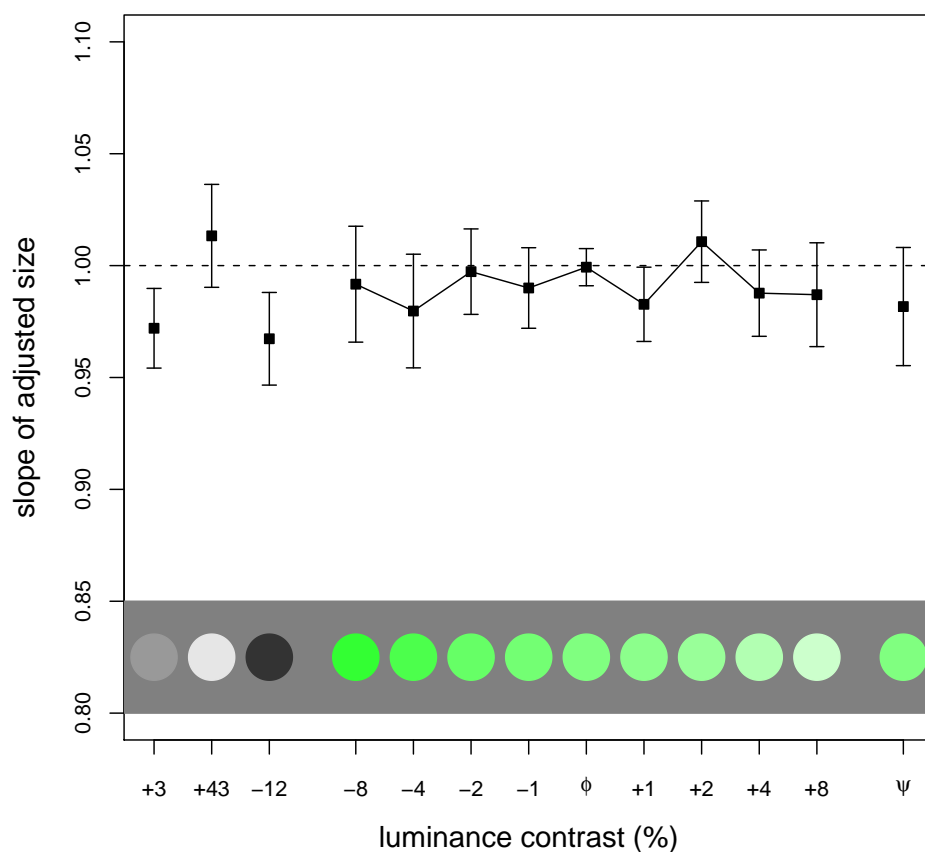


Figure 2.5: Mean slope of adjusted disc size in the different color conditions. Values on the abscissa depict the luminance contrast with the background in percent. Φ : photometric isoluminance. Ψ : subjective isoluminance. Errorbars are ± 1 standard error of the mean (between subjects). The dashed line represents unity scaling.

found in the only study with significant effects of viewing condition on MGA slope we are aware of. Here however, we found an increased slope with constant average MGA. The slope for the perceptually isoluminant targets was 1.14. Interestingly, this comes closer to a physically perfect scaling than do the slopes found in most other conditions. However, we don't think that size information obtained from isoluminant targets is more veridical than for luminance targets. Such an effect

should also be seen in the perceptual data which was not the case in our study.

All other measures of grip quality did not show significant differences between the isoluminant targets and the other ones. Neither MT, RT, the timing of MGA or the variance in the movement path were affected by the color of target stimuli. Our findings are in line with the results of White, Kerzel, and Gegenfurtner (2006) who found no differences in movement accuracy and latency between isoluminant and non-isoluminant targets as did Anderson and Yamagishi (2000) and Braun et al. (2008). White et al. (2006) also critically reviewed earlier studies reporting longer latencies for isoluminant stimuli in a reaction-time task involving button presses (Burr, Fiorentini, & Morrone, 1998; Schwartz, 1992) or saccades (Perron & Hallett, 1995; Satgunam & Fogt, 2005; van Asten, Gielen, & de Winkel, 1988). Isoluminant stimuli thus do not seem to generally delay motoric responses although Braun et al. (2008) recently reported such a delay for smooth pursuit eye movements on isoluminant targets.

Assessing the perceptual size estimates we found that the two achromatic stimuli with +3 and -12 percent of background luminance led to smaller size estimates than many of the other. It is known that size perception may depend on the luminance of a stimulus especially for low-contrast stimuli (Kulikowski, 1975; Gelb & Wilson, 1983; Georgeson, 1985; Davis, Kramer, & Yager, 1986). The fact that the smaller estimated disc size for two of the achromatic conditions was not reflected by a smaller MGA in the grasp task is most likely due to the larger variability of the measure than due to a different processing of stimuli in grasping and in perception.

In summary we conclude that the quality of grasp movements is not profoundly affected by isoluminance of target and background. Since also the finding of a steeper MGA slope in the subjective isoluminance condition does not point to a diminished amount of size information one has to assume that targets solely defined by a chromatic contrast are as suitable for movement planning as targets having a luminance or a luminance and chromatic contrast.

Chapter 3

Delayed pointing and grasping in optic ataxia

Abstract

Several studies have shown a paradoxical effect in the movements of patients suffering from optic ataxia: performance increases when the movement starts delayed and is made without sight onto the target. This effect was reported in pointing as well as in precision grip grasp movements. The timecourse of this improvement in pointing has been assessed by Himmelbach and Karnath (2005). These authors demonstrated that there is a linear decrease in pointing error with increasing delay time. In the present study we aimed at a replication of this finding and an assessment of the according timecourse for precision grip grasping. We measured two optic ataxic patients (U.S. and R.W.) in a pointing and a grasping task with immediate movement execution and at different delay times. We assessed the pointing movements with respect to absolute pointing error, angular and amplitude error as well as pointing precision. An improvement due to delay was found only for the amplitude error in Patient R.W.. In grasping we assessed the scaling of maximum grip aperture

to object size and found no improvement with delay in neither patient. As data from preceding studies on the topic show a heterogenous pattern as well we propose an explanation of the delay effect which is different and more parsimonious than the current standard explanation which is based on the A. D. Milner and Goodale (1995, 2006) two-visual systems hypothesis. We argue that a single visual system together with an elongated speed-accuracy trade-off in patients can account for all of the available data.

3.1 Introduction

Optic ataxia is a neurological condition characterized by gross errors in visually guided reaching. The first account on the condition was given by Bálint (1909). He reported on a patient with intact vision who nevertheless had considerable difficulties with visually guided actions like for example cutting meat with a knife. Movements not directly guided by vision, like reaching out for the own ear, however, remained accurate in this patient. Since this first report on optic ataxia several accounts of different cases have been given. The condition has been described in patients with bi- as well as unilateral lesions. Perenin and Vighetto (1988) demonstrated that in unilateral lesioned patients the deficit is found in the contralesional visual field when reaching with either hand (field effect) and when a reach is done with the contralesional hand in either visual field (hand effect). Most of the time the visuo-motor deficits of patients are confined to the visual periphery and movements to foveated targets are largely unimpaired. Generally optic ataxia arises from lesion in the posterior parietal cortex. However, a variety of affected areas has been reported in different cases. By overlaying the lesion sites from several patients Perenin and Vighetto (1988) found the intraparietal sulcus (IPS) to be involved in all of the cases and the superior parietal lobule (SPL) in most of them. They thus considered these areas to be the core locations responsible for the disorder. A more recent

metaanalysis (Karnath & Perenin, 2005) identified the junction between superior occipital cortex and the inferior parietal lobule (IPL) as well as the junction between the occipital cortex and the SPL along with the precuneus as being the core areas.

In recent years cases of optic ataxia have received particular attention as they can serve as a means for drawing conclusions about the mechanisms of vision and visuo-motor transformations for action. This is especially true within the framework of the A. D. Milner and Goodale (1995) hypothesis of two streams or pathways for visual processing. These authors, drawing on earlier work of Trevarthen (1968), Schneider (1969) and most notably Ungerleider and Mishkin (1982), propose the existence of one ventral visual stream responsible for the conscious representation of our surroundings (vision for perception) and one dorsal visual stream responsible for visual guidance of movements (vision for action). Mainly due to the proposed coupling of the two streams with the parvocellular and magnocellular layers of the lateral geniculate nucleus they are thought to convey different aspects of the visual information. The ventral stream is believed to carry neural signals from the parvo- as well as magnocellular layers and reaches the inferotemporal cortex (IT) via area V4. It propagates information of low temporal resolution and its areas have relatively poor ability to code the location of objects in absolute metrics as receptive field sizes of their cells are large. Location of objects is thought to rather be represented in a relational way. Chromatic sensitivity and spatial resolution, however, are high in the ventral stream areas as object recognition is one of their major concerns. The dorsal stream on the other hand is proposed to receive visual information mostly from the magnocellular layers and reaches the posterior parietal region mainly via the medio-temporal area (MT). Dorsal stream areas thus have low sensitivity for color but a good temporal resolution and are believed to operate on an absolute metric for object localization.

Empirical evidence for this theory has been presented from anatomical studies, monkey physiology and behavioral studies in the human. An important cornerstone are studies of patients with neurological disorders (most notably Goodale & Milner,

1992; Goodale et al., 1994). Goodale et al. (1994) reported a double dissociation of a perceptual recognition task and a visually guided grasp task in a pair of patients suffering from visual agnosia (patient D.F.) and optic ataxia (patient R.V.) respectively, supporting the proposed division between the two visual streams (but see Pisella, Binkofski, Lasek, Toni, and Rossetti (2006) and Pisella et al. (2009) who propose a more complex modular model for these findings). In their study D.F. was able to choose appropriate contact points when picking up differently shaped discs but she could not perceptually discriminate those discs from each other. In patient R.V. the opposite pattern was observed, she being able to perform the discrimination task while failing in the grasp task. Goodale et al. (1994) proposed that D.F. suffers from a selective ventral stream disruption while in R.V., the optic ataxic patient, the dorsal stream processing is compromised. Subsequent to this study behavioral data of optic ataxic patients was also used to assess the proposed temporal properties of the two visual systems. A paradoxical but theory-consistent effect of delay in visuomotor tasks was found by several authors: A. D. Milner, Paulignan, Dijkerman, Michel, and Jeannerod (1999), A. D. Milner, Dijkerman, McIntosh, Y., and L. (2003), Revol et al. (2003), Rossetti et al. (2005), Himmelbach and Karnath (2005), Rice et al. (2008) and Himmelbach et al. (2009) reported from a total of six cases of optic ataxia (patients A.T., I.G., O.K., M.H., U.S. and G.H.) that pointing errors decreased when the movement was not carried out directly but after a delay and from memory in absence of the target. Measurements of optic ataxic patients on grasp movements showing the same effect were reported by A. D. Milner et al. (2003). These authors assessed the maximum grip aperture (MGA), which is the widest opening between the two fingers participating in a precision grip during the movement (Jeannerod, 1984, 1986). Normally this measure is linearly related to the final grip aperture and thus can serve as a mean to estimate if size information about the target object is available in the brain for motor planning purposes. A. D. Milner et al. (2003) could show that patient I.G. had improved MGA scaling in a pantomimed and a real grasp task after five seconds delay as compared to immediate

movement execution.

As an explanation for these paradoxical findings it was suggested that all participants, including the optic ataxic patients, normally use the dorsal stream for guiding actions to visible targets (A. D. Milner et al., 1999; A. D. Milner & Goodale, 1995). Due to the lesion to their dorsal stream areas, however, patients show the large errors observed in their immediate movements. Removing the target from vision, in contrast, enables patients to use their ventral representation of it for guiding the action, given that an appropriate time interval has passed as the ventral areas operate more slowly than the dorsal ones. In subsequent studies this explanation was generally accepted (Revol et al., 2003; Rossetti et al., 2005; Himmelbach & Karnath, 2005) although it was questioned more recently by Himmelbach et al. (2009).

The timecourse of the improvement of delayed movements has been investigated more thoroughly by Himmelbach and Karnath (2005). They measured two optic ataxic patients (U.S. and G.H.) in a delayed pointing task and varied the delay duration between zero and ten seconds. In both patients pointing error linearly decreased with delay time. Himmelbach and Karnath (2005) interpreted these findings as being consistent with a slow, gradual switch between dorsally and ventrally guided movement planning.

The aim of our study was to replicate the findings of Himmelbach and Karnath (2005) for pointing and in addition to establish the timecourse of error decrease for grasp movements. Grip planning, including the preplanning of the MGA, relies partly on different cortical areas as does reaching (Binkofski et al., 1998). Contrary to pointing it also requires the consideration of intrinsic object properties like object orientation and not only the objects position, which is an extrinsic property. It thus is an interesting question if the abovementioned effect of decreasing error with longer delay can also reliably be found in the grasp movements of optic ataxic patients and if it follows the same timecourse as compared to a pointing task.

3.2 Method

3.2.1 Participants

We measured two female patients (U.S. and R.W., 69 and 65 years old) suffering from optic ataxia and eight healthy controls of similar age. One of the controls was excluded from analysis due to gross misreaching. The final control group thus consisted of seven participants, four male, with a mean age of 63 years.

Patients and control participants were right handed according to the Edinburgh inventory (Oldfield, 1971). All participants gave informed consent to the experiment which was approved by the local ethics committee and in accordance to the 1964 declaration of Helsinki. Controls were paid an allowance of 10 EUR for their participation.

U.S. was diagnosed with multiple infarcts in the supply area of the left medial cerebral artery in 2001. Subsequent MRI revealed bilateral lesions of the parietal cortex, the left occipito-temporal cortex, left inferior frontal gyrus and smaller parts of the post-and precentral gyri with underlying white matter (see figure 3.1 for anatomical scans of both patients). In the aftermath of the incident she suffered from right hemiplegia, right-sided spatial neglect, simultanagnosia and full field optic ataxia (see also Himmelbach & Karnath, 2005 for a description of this case). When we measured her in 2008 she had recovered from neglect and simultanagnosia but not from optic ataxia and still showed a right hemiparesis of degree 2-3.

R.W. suffered from stroke in March 2008, a few days before we collected the data reported here. She showed left hand and visual field specific optic ataxia along with a left hemiparesis of degree 2-3 and a proprioceptive deficit of the left arm.

3.2.2 Setup and stimuli

Participants were seated in front of a table with an inclined panel affixed to it (see figure 3.2). The head position was fixed by means of a chinrest and we were able to obscure direct view to the panel by means of a liquid crystal shutter glass window

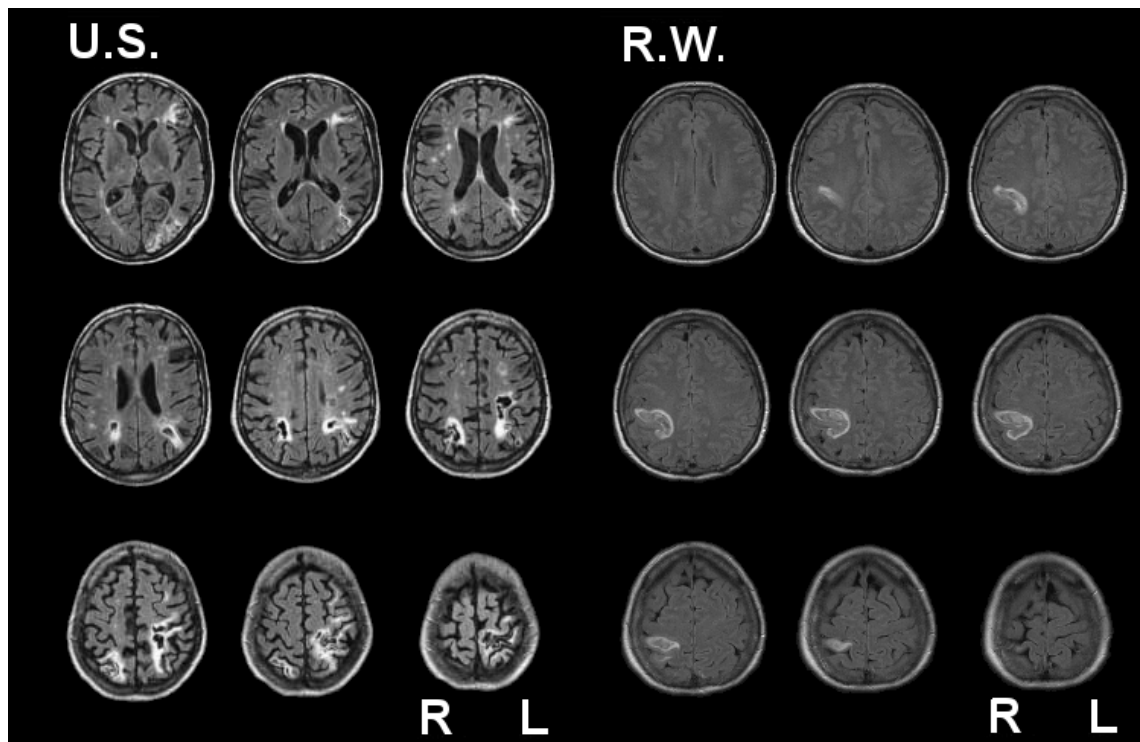


Figure 3.1: MRI scans of patients U.S. and R.W. L = left; R = right. Scans of both patients were conducted directly following confinement to hospital and thus depict the situation right after the individual incidents occurring 2001 (U.S.) and 2008 (R.W.) respectively.

(PrivaLite, St. Gobain Glass) which was installed between subject and table and whose transparency could be changed from clear to opaque. On the near end of the inclined panel, adjusted to the midline of the participants body, there was a hemispherical knob which served as a starting point for all movements. Also along the midline a green LED was attached to the panel and served as a fixation point in trials where fixation was required. The fixation LED was bright enough such that participants could still see it when the shutter glass was in its opaque state. On the left side of the panel three more red LEDs were installed at a distance of 5 cm to each other and served as target points for pointing and grasping movements. The distance between the starting point and the center target LED was 24 cm. We used three bars of plexiglas as stimuli for the grasp movements. They were all 2 cm in

height and width and were 2, 4 and 6 cm in length. We measured grasping and pointing movements with an acoustic motion tracking system (Zebris CMS20) with a sample frequency of 120 Hz. Two markers of the system were fixated to the nails of the left thumb and index finger respectively. In experimental conditions where participants were required to fixate the central fixation LED one experimenter was seated on each side of the participant and monitored eye gaze.

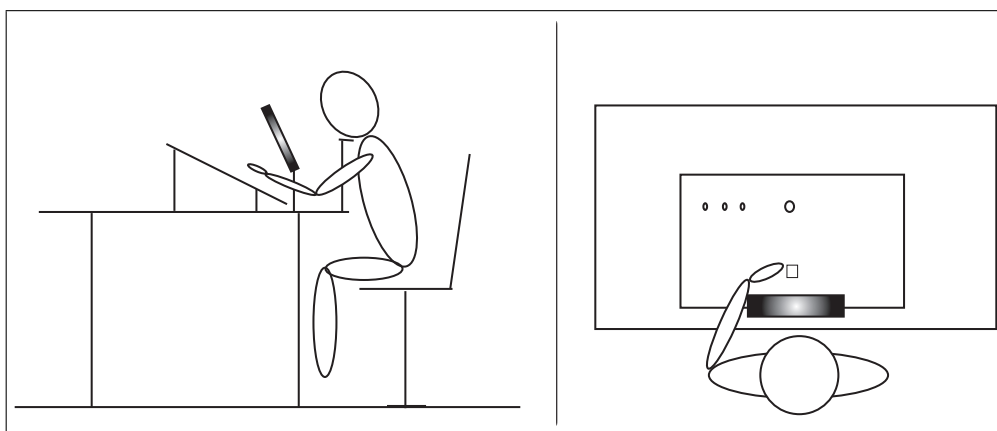


Figure 3.2: Setup seen from the side and from above. The swatched rectangle indicates the position of the shutter glass window. Target LED positions are marked by the three small circles on the left side of the panel. The larger circle in the center marks the position of the fixation LED. The small square shows the position of the starting point for every movement.

3.2.3 Procedure

After filling in the informed consent form participants received the instructions. For the grasping task these contained directives on using a precision grip of index finger and thumb only. For both tasks participants were asked to make quick and accurate movements. Afterwards participants accomplished four baseline conditions (pre baseline) which are described in detail below. After the baseline measurements the delay conditions were performed and then a repetition of the four baseline conditions followed (post baseline). In every condition the trial started when the shutter glass

window switched from the opaque to the transparent state. Participants then had three seconds of clear view onto the experimental panel and the stimulus. A beep signal was always the indicator that the required movement should be started.

In the pointing task one of the three red peripheral LEDs was lighted when the window opened and indicated the target for pointing with the index finger. In the grasping task one of the three plexiglas bars was placed on the central one of the three peripheral LEDs with its longer axis pointing towards the start point. Illumination of the LED under the bar resulted in an illumination of the whole object because the surfaces of the bars were roughened and thus diffused the light. The bar had to be grasped with a precision grip of index finger and thumb of the left hand and carried to a target area which was directly adjacent to the left side of the panel.

In the baseline conditions the acoustic go signal for the movement occurred directly after the first three seconds of clear view and participants then had four more seconds to execute the movement while the shutter glass remained open. Then the shutter glass turned opaque and the trial was finished. In the first two, the *free view* baseline conditions, participants were allowed to freely explore the target with their gaze while carrying out the grasping (1st condition) or the pointing (2nd condition) movement. In the following two, the *fixation* conditions, the green midline LED was switched on and participants were required to grasp (3rd condition) or point (4th condition) while fixating it. All baseline conditions consisted of four trials per stimulus which resulted in 12 trials per condition.

In the delay conditions the shutter glass turned opaque and the target LED was switched off after the initial 3 seconds of clear view. The signal for movement start then occurred after a variable interval of 0, 2, 5 or 10 seconds. Participants thus had to execute the movement blindly under visual open loop conditions. Central fixation was required for all trials. We measured two blocks of grasping and two blocks of pointing movements. One block had three trials for every target and delay which sums up to 36 trials per block and 144 trials total for most of the controls. The patients and one control participant completed three blocks of grasping and

pointing instead of two which resulted in a total of 218 trials.

After completing the delay conditions the four baseline conditions were repeated. One of the control participants reported strong fatigue at this point of the experiment and thus did not complete these post baseline measurements. Except for patient R.W., who was measured on two subsequent days, data collection for all participants was completed on one day in one session of about two hours length. After the experiment participants filled in the handedness questionnaire.

3.3 Results

The main measures of interest for our analyses were the MGA for grasping and the final endpoint of the movement for pointing. Statistical analyses were conducted using the statistics package R (R Development Core Team, 2008), its package for mixed effects models (Pinheiro, Bates, DebRoy, Sarkar, & R Core team, 2008) and the |STAT tools (Perlman & Horan, 1986).

3.3.1 Pointing

In pointing we analysed all measures of pointing error reported in previous studies on the delay effect. These are: absolute pointing error, directional error, amplitude error and pointing precision. We focused, however, on absolute pointing error which is the euclidian distance between the end point of the movement and the target LED. The end point was defined as being the first point of resting after movement onset. Figure 3.3 shows these errors in the four baseline conditions. We used the Bayesian Standardized Difference Test (Crawford & Garthwaite, 2007) to test if this error increased between fixation and free view conditions more strongly in patients than in controls. The bayesian method provided by the same authors was used for testing of absolute differences of performance between patients and controls. Please note that the latter method makes a one-sided test by default. We found significantly

larger error increases between free view and fixation condition for R.W. (pretest: $p = .029$, posttest: $p = .037$) and U.S. (pretest: $p = .002$, posttest: $p < .001$). We also found significantly larger pointing errors in patients compared to controls in the fixation conditions (R.W. pretest: $p = .007$, posttest: $p = .018$, U.S. pretest: $p < .001$, posttest: $p = .001$) but not in the free view conditions (R.W. pretest: $p = .335$, posttest: $p = .306$, U.S. pretest: $p < .459$, posttest: $p = .690$). Mean absolute pointing errors for the baseline conditions are depicted in figure 3.3.

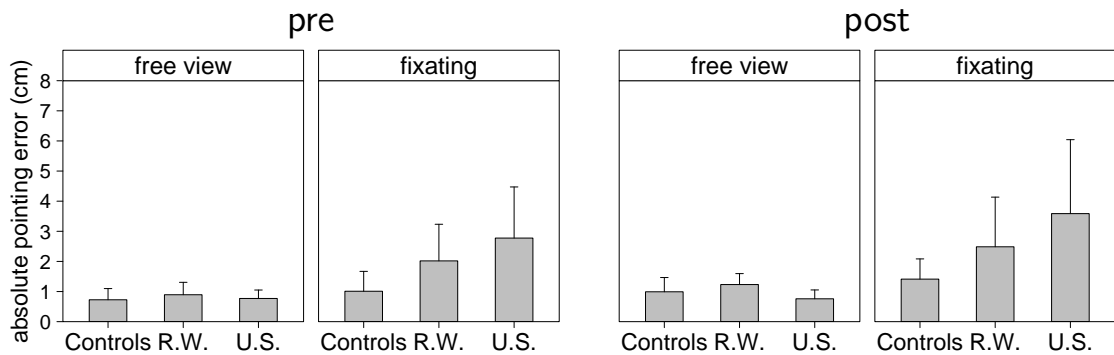


Figure 3.3: Mean absolute pointing error for controls and patients. The two left hand side panels depict data from pre- the two right hand side ones from posttesting. Labels on top of each panel refer to the free viewing and the central fixation condition respectively. Errorbars indicate one SD.

To test the effect of the delay times on pointing error we calculated a linear regression of absolute pointing error over delay times for the individual patient and the control participants as a group. Neither for U.S. ($t_{(105)} = .17$, $p = .858$) nor for R.W. ($t_{(104)} = 1$, $p = .31$) a significant effect of delay on absolute pointing error was found. For the control group we found a positive slope which was significantly different from zero ($t_{(537)} = 2.6$, $p = .008$). The according data are depicted in figure 3.4 with the data of Himmelbach and Karnath (2005) as a comparison.

In order to test if a training effect due to the repeated execution of the pointing task occurred we also calculated linear regressions of pointing error on trial number. There was no significant effect for either patient (U.S.: $t_{(106)} = 1$, $p = .275$, R.W.: $t_{(106)} = .78$, $p = 0.437$). The control participants as a sample, however, showed some

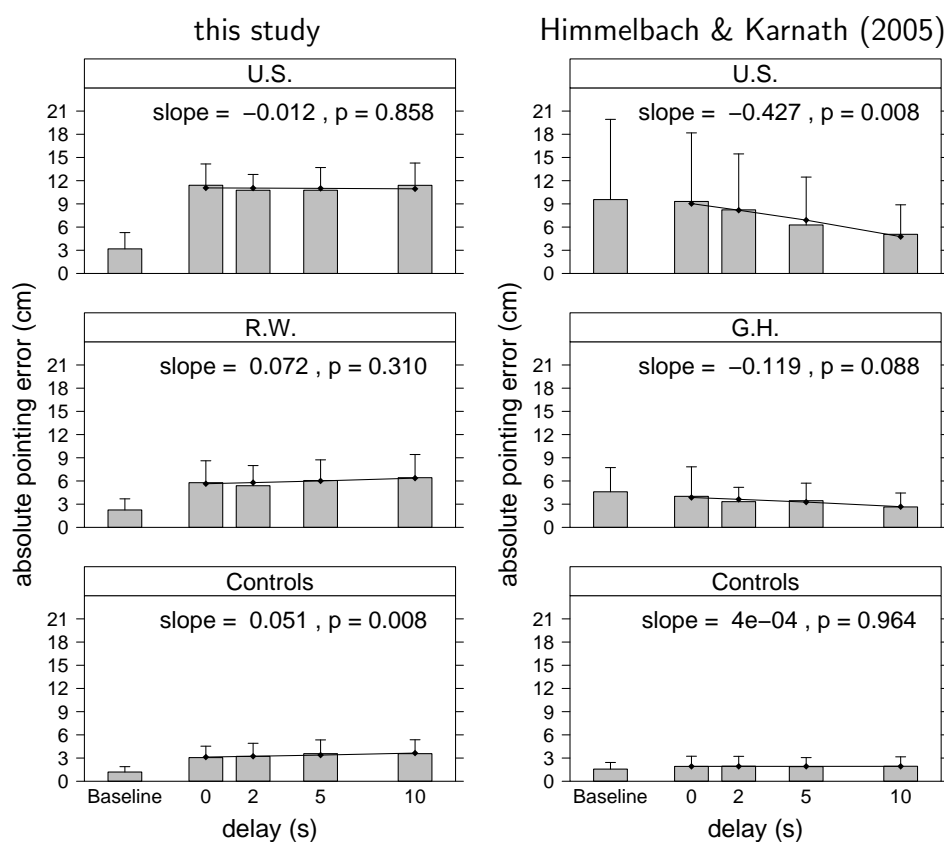


Figure 3.4: Mean absolute pointing error in the delay conditions. The first bar shows data from the pre and post measurements with gaze fixation as a baseline. The remaining bars depict data for the different delay times. The lines and black diamonds are a linear fit to the delay conditions. The numbers in each panel show the slope of this fit and its p -value. Seen on the left hand side are the data from our study. The right hand side shows the data of Himmelbach & Karnath (2005) as a comparison. Errorbars are one SD.

increase in pointing error over the course of the experiment ($t_{(538)} = 4, p < .001$).

As some studies (for example A. D. Milner et al., 2003) have reported improvements in pointing with regard to the angular or directional error we also calculated this measure for the patients individually and for control participants as a group. These data are pictured in figure 3.5 along with the amplitude errors, a measure used in the studies of Rossetti et al. (2005) and Revol et al. (2003). We also calculated linear regressions for these measures. There was no change in angular error

for U.S. ($t_{(105)} = 1.3, p = .185$). We did however find a significant decrease for R.W. ($t_{(104)} = 3.8, p < .001$) who deviated more strongly towards her own midline with longer delay times. An increase of angular error was found for the control participants ($t_{(537)} = 2.7, p = .007$). For the amplitude error we found no effect of delay in patient U.S. ($t_{(105)} = 0.8, p = .423$) while a significant decrease of this error with increasing delay was found in patient R.W. ($t_{(104)} = 4.1, p < .001$). In the control sample no effect was found ($t_{(537)} = 1.4, p = .17$).

U.S.' pointing errors seemed to be somewhat systematic as she exhibited an undershoot in her movements failing to raise her arm as much as necessary which was more pronounced in the delay conditions than in the baseline measurements. For this reason we also explored if there might be an increase in the precision of pointing according to some internal goal point. To this end we calculated the absolute distance not from the target LED but from the average individual endpoint for each participant and condition. The results of this analysis are depicted in figure 3.6. We calculated linear regressions for each patient and the control participants on this absolute internal error. There was no decrease in this error measure for U.S. ($t_{(105)} = .8, p = .423$). We did however find a significant increase in this error for R.W. ($t_{(104)} = 3.4, p = .001$) and also for the control participants ($t_{(537)} = 2.4, p = .017$).

3.3.2 Grasping

We used the MGA as the dependent measure in the analysis of grasp movements as its slope in relation to bar length reflects if size information is present in the visuo-motor system and is used for motor guidance. Figure 3.7 shows the MGA as a function of bar length in the baseline conditions. Included in every panel of the figure is a linear regression and the p -value of the according slope as compared to zero. We found significant scaling of MGA to bar length for both patients only in the free view conditions (U.S.: pre: $t_{(10)} = 4.5, p = .001$, post: $t_{(1,10)} = 3.1, p = .011$, R.W.: pre: $t_{(10)} = 5.1, p < .001$, post: $t_{(10)} = 4.7, p < .001$) but not in the

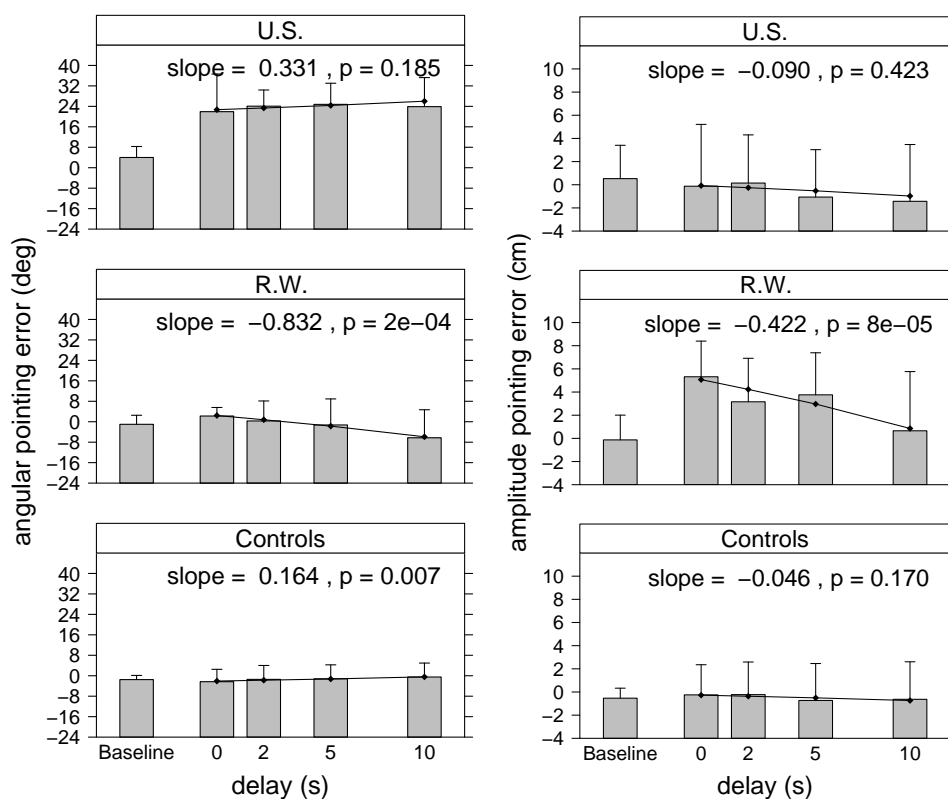


Figure 3.5: Angular and amplitude error of pointing movements in the delay conditions. On the left hand side the mean angular pointing error from the target LED is drawn. Negative values denote movements which are biased towards the saggital plane. On the right hand side the amplitude error is drawn. Positive values indicate an over- negative values an undershoot in the movement. The leftmost bar of each panel shows data from the pre and post measurements with gaze fixation as a baseline. Lines and black diamonds are a linear fit to the data of the delay conditions. The numbers in each panel show the slope of this fit and its p -value. Errorbars are one SD.

fixation conditions (U.S.: pre: $t_{(10)} = 0.22$, $p = .829$, post: $t_{(10)} = 1.7$, $.123$, R.W.: pre: $t_{(10)} = 0.79$, $p = .447$, post: $t_{(10)} = 0.63$, $p = .543$). For the controls significant scaling to bar length was found in all conditions (pre free view: $t_{(82)} = 18$, $p < .001$, pre fixation: $t_{(82)} = 8$, $p < .001$, post free view: $t_{(70)} = 12$, $p < .001$, post fixation: $t_{(70)} = 12$, $p < .001$).

Figure 3.8 pictures the data of the delay conditions and also of the pre and

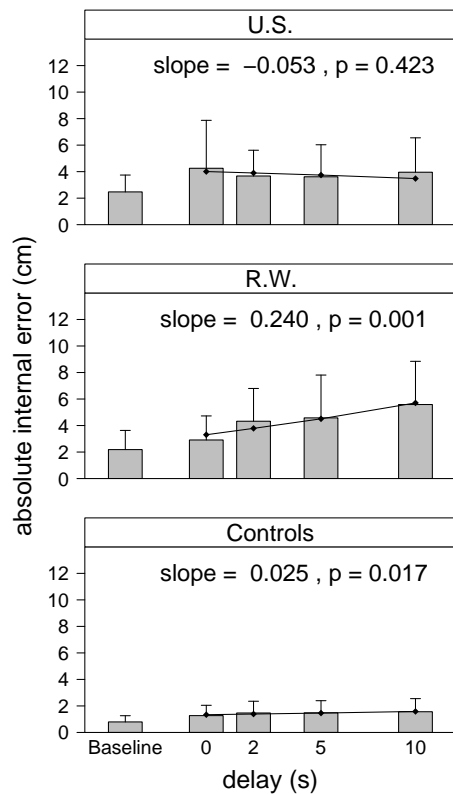


Figure 3.6: Absolute internal error of pointing movements in the delay conditions. The absolute internal error is the mean distance to the average hit-point of the particular subject and condition. Lines and black diamonds are a linear fit to the data of the delay conditions. The numbers in each panel show the slope of this fit and its p -value. Errorbars are one SD.

post fixation conditions pooled as a baseline measure equivalent to figure 3.3 for the pointing data. Each panel shows a linear fit to the data it contains. For the patients none of the slope coefficients was significantly different from zero (all $p < .05$). Contrariwise controls showed significant grip scaling throughout all conditions. In order to test for slope differences between delay conditions of the control participants we calculated a linear mixed effects model (Pinheiro et al., 2008) with bar length as a covariate, delay time as a fixed effect and individual random effects for intercept and slope for every control participant. We found no significant interaction between delay and bar length indicating the same scaling behavior to bar length at all delay

times ($t_{(530)} = 0.558$, $p = 0.577$).

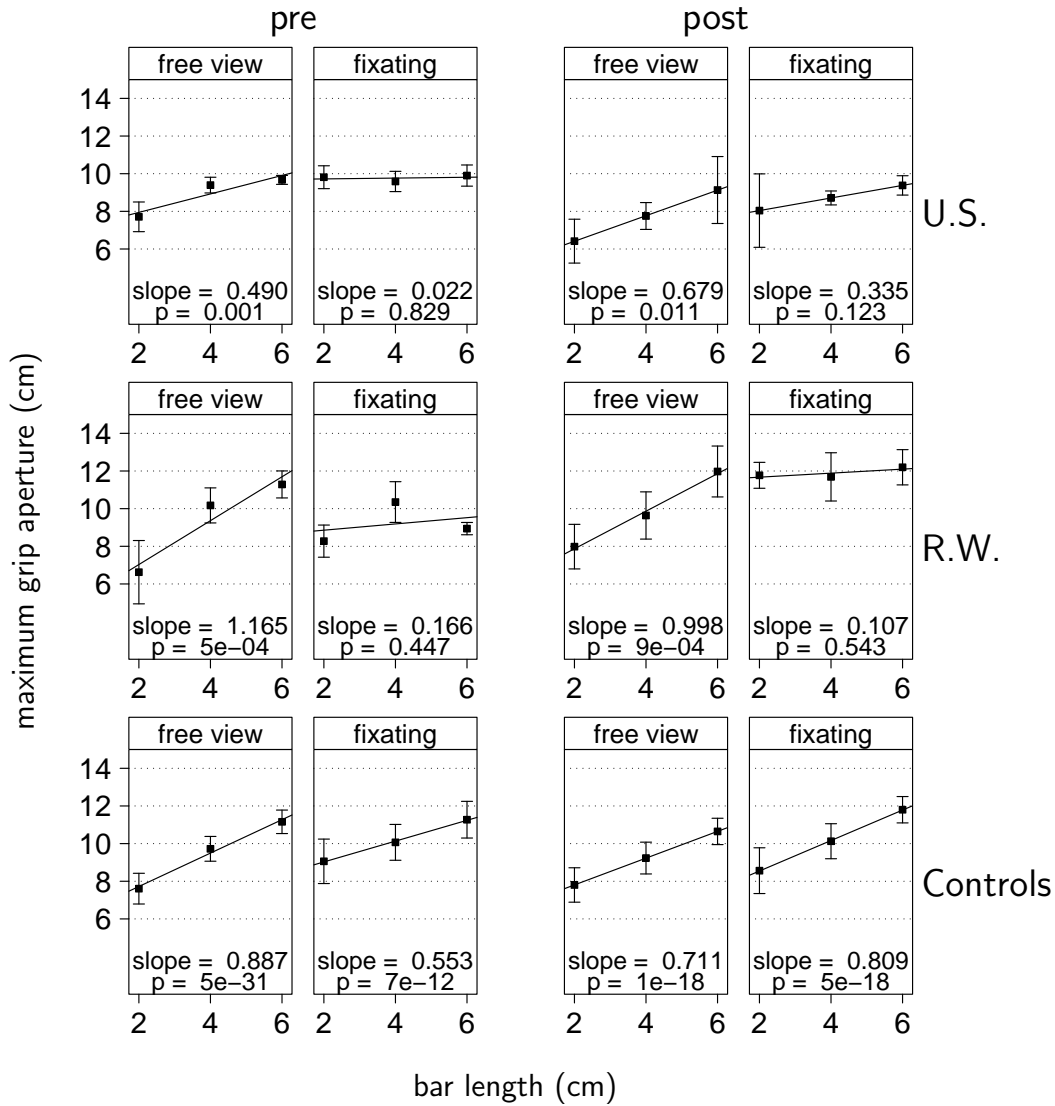


Figure 3.7: Mean MGA as a function of bar length in the different baseline conditions. The first two columns depict data from pre- the last two from posttesting. Labels on top of each panel refer to the free viewing and the central fixation condition respectively (see text). The first and second row depict data of the optic ataxic patients while the last row pictures data of controls. Errorbars are one SD. The solid line shows a least-squares linear regression fit. Numbers in each panel denote the slope of the regression and the p -value for this slope.

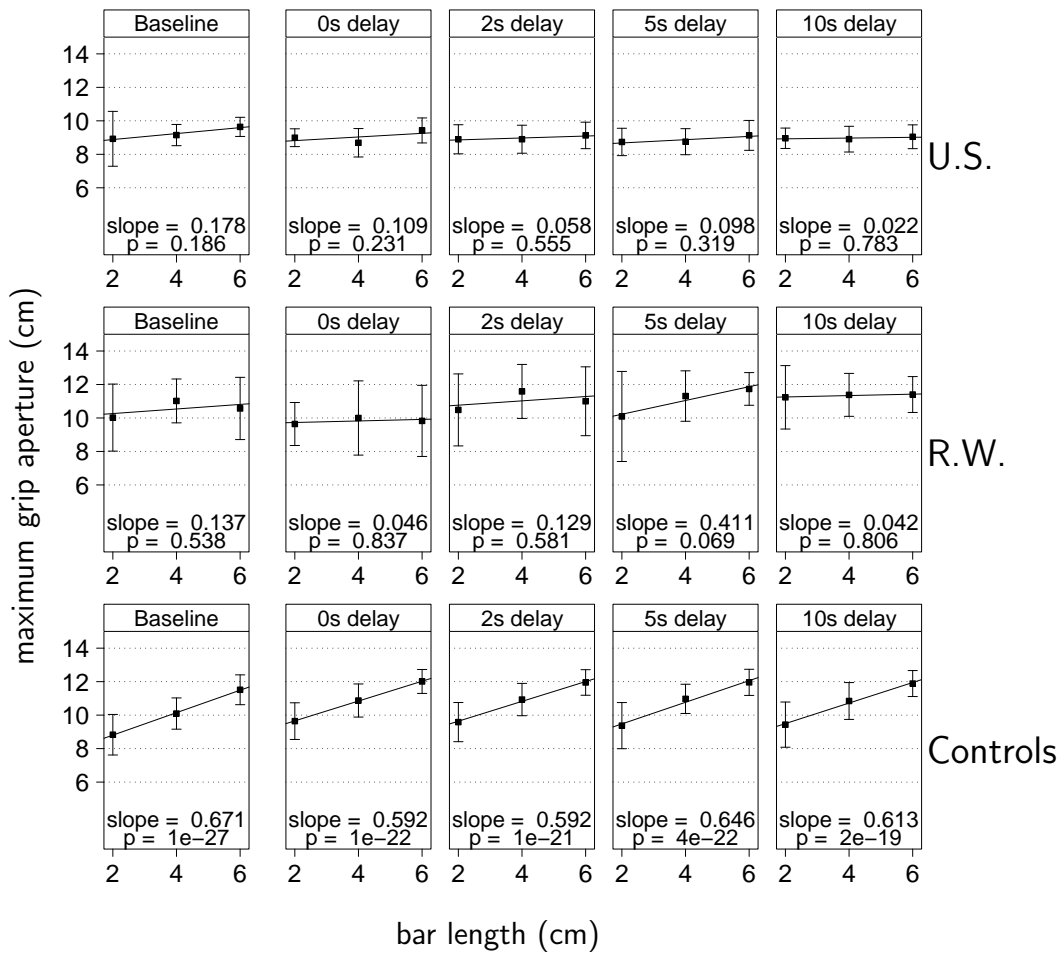


Figure 3.8: Mean MGA as a function of bar length in the different delay conditions. The first column shows data from the pre and post measurements with gaze fixation. The remaining columns show data from the different delay conditions. First and second row show data of the optic ataxic patients. Data of the last row are from control participants. Errorbars are one SD. The solid lines show least-squares linear regression fits. Numbers in each panel denote the slope of the regression and the p -value for this slope.

3.4 Discussion

We analysed data of seven control participants and two optic ataxic patients. Our aim was to assess the timecourse of improvements in the patients movements over a set of delay times.

In the baseline measurements of U.S. and R.W. we were able to demonstrate

the typical effect of optic ataxia in pointing as well as in grasping movements. In pointing both patients showed exaggerated errors in the fixation conditions when movements were directed to the visual periphery. R.W., however, did not show as huge an effect of optic ataxia in her pointing errors as did U.S.. In grasping we found that scaling of the grip aperture to bar length was only present in the free view conditions but not in the conditions with central gaze fixation for both patients. Control participants on the other hand did scale their hand opening to bar length in the fixation conditions as well.

In the delay conditions we found no effect of the delay on the absolute pointing error of both patients. U.S. as well as R.W. both pointed to the targets with constant mean error across all delay times. This is in contrast to what we had expected from the findings of A. D. Milner et al. (1999), A. D. Milner et al. (2001), A. D. Milner et al. (2003), Revol et al. (2003), Rossetti et al. (2005), Himmelbach and Karnath (2005) and Himmelbach et al. (2009). Moreover R.W. got worse with longer delay times in terms of precision and directional error. An improvement due to delay was only present in the amplitude pointing errors of patient R.W..

Data of earlier studies where delay effects in grasping or pointing could be demonstrated come from six different optic ataxic patients and the effect was established using four different measures of pointing error. Below we will shortly review these findings grouped by case:

Patient A.T. suffered from an eclamptic attack at age 32 and shows relatively widespread lesions in both parietal lobes. Data of her from a delayed pointing task were reported by A. D. Milner et al. (1999), A. D. Milner et al. (2003) and Rossetti et al. (2005). Data from a delayed grasping task were measured but not reported by A. D. Milner et al. (2003). A.T. showed a decrease in absolute pointing error following a delay of five seconds as compared to no delay in the study of A. D. Milner et al. (1999). A. D. Milner et al. (2003) did also report a decrease in pointing error following a delay of five seconds. In contrast to the A. D. Milner et al. (1999) study, however, they measured the angular deviance from the pointing target instead of

absolute pointing error. While the effect in A. D. Milner et al. (1999) is very clear cut its harder to judge in the A. D. Milner et al. (2003) study and outcomes of statistical analyses are not reported. The third study with A.T. as a participant was done by Rossetti et al. (2005). These authors report improvements in absolute pointing error and amplitude of the pointing movement but no improvement in angular error was found. From their graphical presentation of the data also an improvement in the variability of the movement as represented by a confidence ellipse area can be inferred although this measure was not subject to a statistical test.

Patient I.G. to the best of our knowledge is the only patient from whom a delay effect in grasp movements was reported (A. D. Milner et al., 2001, 2003). She suffered from bilateral parieto-occipital infarction at age 29 with lesions in BA 7, 18 and 19, the intraparietal sulcus and part of BA 39. She participated in the studies of A. D. Milner et al. (2001) (part of the same data was also reported in A. D. Milner et al., 2003), Rossetti et al. (2005) and Himmelbach et al. (2009). A. D. Milner et al. (2001, 2003) conducted an experiment which required her to grasp objects in an immediate grasp without delay, in a real grasp which was delayed by five seconds or in a pantomimed grasp which was delayed by five seconds. They also asked her to do a manual size estimate of the same objects where she opened her fingers as wide as she perceived the object to be large. It was reported that grip scaling to object size was present in the manual size estimation task, the pantomimed condition and also, but not as good, in the delayed real grasping task. No grip scaling was found in immediate grasping. The differences are interpreted as a support for the A. D. Milner and Goodale (1995) two-visual-streams hypothesis with the better performance in the delayed and especially the delayed pantomimed task being thought to be mediated by ventral areas. It is important to note, however, that these authors conducted their experiment in an abccba design where “a” stands for the blocks of immediate grasping. From visual inspection of their results (A. D. Milner et al., 2001, figure 3(a), A. D. Milner et al., 2003, figure 5(a)) it seems that scaling was only absent in the first, but not the second block of immediate grasping. It could

thus be possible that the first few trials simply reflect a missing accommodation to the task at the beginning of the experiment and that the scaling behavior otherwise is present in all of the conditions.

A. D. Milner et al. (2003) also acquired data of patient I.G. in a delayed pointing task. As for A.T. these authors report an improvement in angular error also for I.G.. Results from statistical testing, however, are not given. I.G. was also measured in a delayed pointing task by Rossetti et al. (2005). From all of their dependent measures—absolute pointing error, angular error, amplitude error and variability as the area of a confidence ellipse—they reported a significant improvement due to delay only in the angular error and only for the most eccentric pointing targets. From visual inspection of their data it nevertheless can be assumed that also the area of the confidence ellipse might have been significantly reduced by introducing the delay (Rossetti et al., 2005, figure 5). Finally I.G. participated in the study of Himmelbach et al. (2009). As a dependent measure these authors assessed the absolute pointing error. They found the differences of the means between delayed pointing and immediate pointing to be consistent with an improvement due to delay in the relevant hand/visual field combination.

Patient O.K. was tested by Revol et al. (2003). He suffered from ischemic stroke at age 32 or 33 and received rather confined damage to the right posterior parietal lobe along with a slight damage to the right posterior part of the corpus callosum. In a delayed pointing task he showed no improvement in absolute pointing error or pointing angle (in fact he got worse on the latter). He did show an improvement in movement amplitude error and in the area of the confidence ellipse for pointing endpoints (note that these two measures are very likely correlated).

U.S. was a case reported by Himmelbach and Karnath (2005) and also measured in this study. The medical details have been mentioned above and in Himmelbach and Karnath (2005). Her age at the stroke incident was 62 years. In the study of Himmelbach and Karnath (2005) a significant improvement in absolute pointing error with longer delay times was reported while other measures of pointing error

were not applied. In the data of her presented here we found no improvement in our different measurements of pointing error and also not in grasping.

G.H. is another patient presented by Himmelbach and Karnath (2005). She was 57 when she suffered from stroke which was followed by a relatively confined lesion to the left medial parietal cortex, mainly the precuneus. Also for her a significant improvement on absolute pointing error with longer delay times was reported. It should be noted however, that statistical significance in her case was only reached by applying a one-sided test. Since an increase in error is not an uncommon finding when applying a delay neither for healthy controls (see for example Himmelbach et al., 2009) nor for patients (as it was found for example in R.W. in this study or partially in O.K. by Revol et al., 2003) results from one-sided testing should be taken cautiously.

The last patient reported here as having been measured in a delayed pointing task was M.H.. M.H. was also measured in a study of Cavina-Pratesi, Ietswaart, Humphreys, Lestou, and Milner (2010) who describe his lesions as resulting from an anoxic episode which led to damage in posterior parietal and frontal regions with a special emphasis on the intraparietal sulcus of the left hemisphere and extending to the medial aspect and the inferior parietal lobule. He was also reported to have subcortical and cortical atrophy in the left hemisphere, located in the posterior parietal, fronto-temporal and frontal regions as well as the lentiform nucleus and claustrum. Rice et al. (2008) measured this patient in a delay task which differed somewhat from those of the abovementioned studies. In their experiments M.H. had to avoid obstacles during pointing. The authors found that introducing a delay of five seconds significantly improved his performance on the task.

From this short overview of the reported cases it can be concluded that there is not one single effect of improvement in delayed movements which is reliably found across patients. Some of the patients show improvements in certain error measures while others do not. Seemingly improvement with delay is not even stable within single patients as Rossetti et al. (2005) did not find an improvement of absolute

error in I.G. while Himmelbach et al. (2009) did and Rossetti et al. (2005) did not report an improvement in A.T. on angular error while such an improvement was found by A. D. Milner et al. (2003)

Finding an effect of delay might be related to the severeness of the lesion since a convincing improvement in absolute pointing error was found especially in A.T. and U.S., both patients with rather extensive, bilateral lesions while unilaterally lesioned patients O.K. and R.W. showed no effect on absolute pointing error and G.H. only a weak one. From inspection of the according figures of A. D. Milner et al. (1999), Revol et al. (2003) and Himmelbach and Karnath (2005) also the conclusion can be drawn that A.T. and U.S. exhibited much stronger absolute pointing errors as did O.K., R.W. and G.H. in the first place. This of course also gives those patients more room for improvement in the delay conditions. These circumstances can also be considered as a possible explanation for the absence of the delay effect in the unilaterally lesioned R.W. who was measured here although it should be noted that absolute error levels of this patient nevertheless were above those of G.H. in Himmelbach and Karnath (2005). A final decision, why a delay effect on absolute pointing error couldn't be demonstrated in this patient cannot be made from the available data.

It is also not possible to arrive at a definite explanation for the differences in U.S.' performance between this study and the measurements reported by Himmelbach and Karnath (2005). It should be noted, however, that we obtained data from her at an age which was considerably higher than that of all the other reported cases showing the delay effect. Moreover data of the Himmelbach and Karnath (2005) study were acquired soon after she received her lesion while here we collected the data seven years later such that restructuring processes of the brain might have taken place between the measurements. Neuropsychological assessment prior to our experiment also revealed a very low capability in a test of visual short term memory where the subject is asked to repeat the sequence in which the experimenter touches some objects. Unfortunately there were no measurements on this test from her acute

phase available so it is not clear if her memory abilities have changed or have been already as low back then.

How does our study contribute to the elucidation of the mechanisms at work in delayed movements of optic ataxic patients? From our own data and the data of other patients summarized above we conclude that the delay effect is quite variable in patients suffering from optic ataxia. Of course individual lesions also differ between persons. However, none of the reported patients suffered from mentionable lesions to areas assigned to the ventral stream. It is therefore a straightforward assumption that they should all be able to retrieve similar information from their ventral areas for guidance of the delayed movements. Therefore improvement should take place on the same dependent measures, maybe in magnitude gradually dependent on lesion size. As this does not seem to be the case we propose a different, more parsimonious explanation of the findings: The same visuo-motor system could be responsible for guiding all movements, delayed or not, in patients as well as controls. Damage to this system, as it is present in optic ataxia, simply leads to slower processing, gradually depending on the severeness of the lesion. When the system is given more time for processing the outcome gets more accurate. The aspects of the movement in which improvement is possible may depend on the individual lesion. A speed accuracy trade off like this is a common finding in healthy participants and there has been considerable advancement on understanding its neural basis over the last years (see Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2010, for a review). We propose that in patients suffering from optic ataxia such a process may just take place on a broader timescale and may asymptote at a poorer final outcome level than in healthy participants. From the behavioral data available it seems at least unnecessary to invoke a second mechanism like the pulling of additional information from a ventral route which is normally not involved in motor tasks. We recognize that this standard interpretation of the delay effect which was proposed by A. D. Milner et al. (1999) and which supports the A. D. Milner and Goodale (1995, 2006) two-visual-systems approach is not contradicted by the data. However it is also not

a parsimonious explanation for them.

A. D. Milner et al. (1999) reject this simple explanation for the delay effect for two reasons. Firstly they argue that one should see an improvement with longer delay times in healthy participants as well as in patients. We argue, however, that processing in healthy participants is so fast that such an improvement will not be captured by the standard design employed in practically all of the studies on delayed movements in optica ataxia. Apart from Himmelbach and Karnath (2005) and our own study in the delay condition always a delay time of five seconds was used. McElree and Carrasco (1999) for example could show, however, that decisions in a visual search task reach asymptotic performance levels within about one second. Thus, even with the delay times employed in our study and the one of Himmelbach and Karnath (2005) it is unlikely that we will see any improvement in control participants due to the prolonged processing time as normal processing already has finished during the preview period. Decay from memory, however, takes place as soon as the target disappears and worsens performance of all participants. According to our simple hypothesis optic ataxic patients may reach their asymptotic level of improvement due to prolonged processing time after several seconds, this time course being captured in the data of Himmelbach and Karnath (2005). As long as this improvement is not outweighed by memory decay we will thus observe that performance gets better as compared to immediate movement execution. As a second argument A. D. Milner et al. (1999) note that usually no improvement over time is observed in other patients with severe visual impairment. We are not aware of any studies addressing this specific claim directly. It has nevertheless been shown that some patients with damage to the CNS can benefit from prolonged processing time. Demaree, DeLuca, Gaudino, and Diamond (1999) for example demonstrated such an improvement in a visual and an auditory task in patients suffering from multiple sclerosis. Furthermore it has been reported that patients suffering from optic ataxia often show longer reaction times than do healthy controls. This finding is a mentionable hint in support of our hypothesis as longer reaction times could serve

as a strategy to prolong the time of stimulus processing before movement initiation. In the abovementioned studies on the delay effect in optic ataxia reaction times are not reported. Jakobson, Archibald, Carey, and Goodale (1991), however, report prolonged reaction times in pointing and grasping from optic ataxic patient V.K.. Also Roy, Stefanini, Pavesi, and Gentilucci (2004) found longer reaction times in a grasp task in optic ataxic patient G.T.. In a task where combined gaze movement and pointing was required Gaveau et al. (2008) found a longer delay in corrective saccades for patient A.T. as compared to the healthy controls. Patient I.G., who was measured in the same study as well, however, did not show the same effect. I.G.s delay on the contrary was even shorter than the delay found in controls. However, the authors report that I.G. also was less accurate and needed significantly more corrective saccades to capture the target. This may also indicate that optic ataxic patients actually can profit from a longer processing time. Reaction time for pointing movements was delayed in both patients in this study.

There is further evidence in support of our simple hypothesis for the delay effect. Himmelbach et al. (2009) did a fMRI study on patient I.G. during a delayed pointing task. They found no evidence for a special ventral stream activation pattern in I.G.s brain when they compared it with the data of a control sample. The authors thus could not confirm that in I.G. ventral areas are recruited in the delayed task as compared to the immediate task. The simple view is also consistent with the results presented by A. D. Milner et al. (2003) who, in addition to the standard delay task, also employed a task where the target for pointing or the target object for grasping respectively was secretly changed during the delay interval in a percentage of trials. They found that the optic ataxic participants were unable to adapt their movements fully to the new target. The authors interpreted these findings as evidence for a processing which gets supplementary information from ventral areas. It is however also consistent with a simple slowing-down of the visuo-motor system. Incompatible with the simple explanation, however, is the *real-time view of action* which emerges from the A. D. Milner and Goodale (1995) two visual systems hypothesis (cf. Hu &

Goodale, 2000; Westwood & Goodale, 2003). It states that information in the areas responsible for visuo-motor transformations (the dorsal stream) is extremely short lived and only meant for execution of actions towards targets which are still visible. According to this view, however, there also should be no smooth change from ventral to dorsal control in memory motor tasks but a rather sharp switch when the ventral stream takes over control in movements towards memorized targets. That this does not happen was shown recently in behavioral studies of grasping under different viewing conditions (Franz et al., 2009; Hesse & Franz, 2009). It rather seems to be the case that information about the target of a movement decays exponentially just like it is observed in other memory tasks as well. Further support for a more unified view onto the visuo-motor system comes from a recent study of Rogers, Smith, and Schenk (2009). These authors adapted their healthy subject to delayed or immediate pointing using prism goggles. The aftereffect of this adaptation was transferred between the conditions which is quite unlikely if different representation for the two kinds of movements would be used.

A simple experiment to tease apart influences of processing time and a switch to the ventral system in optic ataxic patients would be to compare a delayed vision condition with a delayed no-vision condition. In the former participants would have full view onto the object during the delay while the latter would be the paradigm used by the abovementioned delay studies where vision is removed during the delay. Currently the standard comparison is between immediate grasping and delay-with-no-vision grasping. With this comparison no conclusions about the influence of processing time can be drawn.

In our grasp data we could not demonstrate any effect of delay on performance in neither patient. In the work of others (A. D. Milner et al., 2003) an improvement for grasping following a delay has only been described in patient I.G. and this result may also be questionable as has been outlined above. Recently Cavina-Pratesi et al. (2010) in a carefully controlled study with the optic ataxic patient M.H. demonstrated that failure in scaling the grip to target size in optic ataxia may be a

secondary result of misreaching rather than a primary problem of size adjustment. These authors showed that scaling is impaired in this patient when a long distance—which gives rise to the possibility of misreaching—has to be covered. When the distance is short scaling remains intact. Failure to scale thus could rather be a strategy of wider digit opening in order to compensate for a larger error in hand positioning. Cavina-Pratesi et al. (2010) suggest that true misadjustment of digit opening is associated with lesions in the anterior intraparietal sulcus (aIPS) an area which may be spared in optic ataxic patients. This explanation could also account for the pattern observed in patient I.G. who in the study of A. D. Milner et al. (2003) showed good scaling in pantomimed grasping where misreaching is irrelevant and worsened scaling in real grasping where misreaching must be taken into account. Again, in our opinion this is a much more parsimonious explanation for the findings than invoking a ventral stream mechanism thought to be activated during delayed and pantomimed grasping.

Chapter 4

A model on human grasp point selection

Abstract

In the everyday task of grasping our visuo-motor system has to solve an intricate problem: How to find the right ones out of an infinity of possible contact points with the object? The model we present here can solve this problem and predict human grasp point selection by using only a few basic rules. Because usually not all of the rules can be perfectly satisfied we assessed their relative importance by creating simple stimuli which put them pairwise into conflict with each other. With the results from these conflict experiments we made model-based grasp point predictions for a novel set of complex shaped objects. The results show that our model mimicks the human choice of grasp points amazingly well.

4.1 Introduction

Many properties of the human grasp movement have been thoroughly studied. Much knowledge has been gathered about the coupling between visual input and the grasp movement (Goodale, Pelisson, & Prablanc, 1986; Goodale, Milner, Jakobson, & Carey, 1991; Goodale et al., 1994; Whitney, Westwood, & Goodale, 2003), the processing of object features (Ganel & Goodale, 2003), and the cortical control of grasping (Cattaneo et al., 2005). Our knowledge about motor control thus has arrived at a high level and we already have models of arm movements (Harris & Wolpert, 1998) and especially grasping (Smeets & Brenner, 1999) available. To date, however, it was not possible to predict an entire human grasp movement because it remained unclear how humans choose their contact points with an object. This is an amazing fact considering that important properties of the grasp movement like the grip aperture and its maximum which are very well studied (Jeannerod, 1984, 1986; Smeets & Brenner, 1999) seem to secondarily arise from the choice of contact points (Cuijpers, Smeets, & Brenner, 2004). Building upon previous work on human and robotic grasping we now identified the most important rules for choosing those points and combined them into the first quantitative model on human grasp point selection in precision grip grasping.

4.1.1 Force closure

The most important physical constraint in grasping is finding a grasp configuration which is *force closure*. Force closure gives the grip stability. A two-digit grip satisfies this constraint when the grasp axis, a line connecting the contact points, lies within the friction cones resulting from the friction coefficient between object and digits (Nguyen, 1986, Corrolary 3).

This requirement is represented in the *opposition space* (Iberall, Bingham, & Arbib, 1986), the *antipodal point* Chen and Burdick (1993) and the *seed point* (Blake, 1992) concepts which are also used in constructing stable grasps for robotic grippers

(Blake, 1992, 1995; Ponce, Stam, & Faverjon, 1993) where efficient algorithms are available for finding those points (Jia, 2002). Simply stated it means that in grasping with two digits you have to place them opposite to each other onto the object and to places where enough friction is present. If you do so your digits won't slip as soon as grip force is applied.

Force closure is a necessity for grasping. Trying to grasp at points which do not satisfy force closure will fail. In our model we assume that it is the goal of the grasper to be as sure as possible that force closure is granted. This is the case if points on the object surface are chosen which align the grasp axis with the central axes of both friction cones. More formal the sum of the angular deviances of the grasp axis from both friction cone center axes (γ) is expected to be zero ($E(\gamma) = 0$). Panel *a* of figure 4.1 shows two grasps which are both force closure but differ in quality according to this rule.

4.1.2 Torque

The next constraint we identified in grasp point selection is a minimization of the shortest distance between grasp axis and gravicenter of an object. This was suggested earlier by Lederman and Wing (2003) and has already been used as a measure of human grip quality Goodale et al. (1994). It is also included in models on synthesizing stable grasps for robot grippers (Sanz, Inesta, & Pobil, 1999; Mangialardi, Mantriota, & Trentadue, 1996). Minimizing the distance between grasp axis and gravicenter has mainly one advantage to the grasper: it ensures that there are no strong torques acting on the grasp axis when the object is lifted. This in turn means that the object can be hold in equilibrium without much effort.

Torque is the product of force and torsion arm length. When grasping an object the acting force is the product of object mass and the acceleration used in lifting. In order to prevent using post-grasp kinematic parameters like the acceleration in the model we included this rule instead by only calculating the product of object mass and torsion arm length. When the torque rule is perfectly satisfied this value

(τ) is expected to be zero: $E(\tau) = 0$. This is the case when the distance between grasp axis and gravicenter is zero as well. Panel *b* of figure 4.1 shows a good and a bad grasp according to this rule.

4.1.3 Natural grasp angle

Force closure is a physical necessity for grasping. Keeping the torque during object lift small is partly a physical constraint but also partly owed to the human grasper because he might be unable or could find it uncomfortable to apply more force which would counteract the resulting torque. Our last constraint, the natural grasp angle (NGA), on the other hand depends completely on the individual human grasper. The term natural grasp axis was coined for the fact that in a disc, where all grasp axes which align with a diameter of the disc are otherwise equally qualified for grasping, nevertheless a certain orientation of the grasp axis is preferred above all others (Lederman & Wing, 2003). The NGA, being the angle of this axis, reflects the comfort of the grip for the grasper. This becomes obvious when we try to grasp an object with exchanged positions of thumb and index finger. The grasping arm then is concerted in a quite uncomfortable fashion. The NGA thus reflects the most comfortable position of the joints for grasping a certain object.

For this rule we state that people aim to realize their personal NGA which is constant for a certain location in the graspers egocentric space. Therefore we expect the difference between the NGA and the actually realized grasp angle (α) to be zero: $E(\alpha) = 0$. Panel *c* of figure 4.1 shows a suitable and a not so suitable grasp according to this rule.

4.1.4 Formulation of the model

Having spotted the most important rules involved in grasp point selection the question arises how these are combined in order to guide the grip. Deviation from each rule causes either grasp failure or discomfort. We thus assume that rule deviation is associated with a penalty in the motor system.

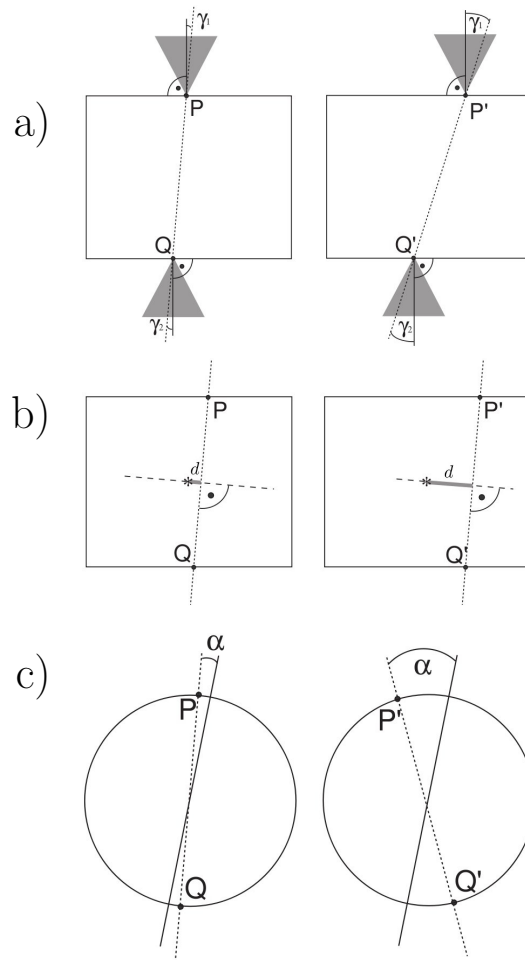


Figure 4.1: Rule examples. The left column shows good grasp point selections P and Q according to the corresponding rules while the grasp points P' and Q' in the right row are not well suited because they create rather large rule deviances. *a)* Force closure rule. A good grasp minimizes the combined angular deviances ($\gamma = \gamma_1 + \gamma_2$) of the grasp axis (dotted) from the friction cones' center axes (solid surface normals in the gray cone area). *b)* Torque rule. The torsion arm (d , grey bar) is the distance between grasp axis (dotted) and gravicenter (*). A good grasp minimizes the product of object mass m and torsion arm, $\tau = m \cdot d$. *c)* Natural grasp angle rule. A good grasp minimizes α , the angular deviance of the grasp axis (dotted) to the natural grasp axis (solid).

Let g be a grasp i.e. an ordered pair of contact points of thumb and index finger. Every g is associated with a certain value of deviance from the friction cone axes $\gamma(g)$, torsion arm times mass product $\tau(g)$ and deviance from NGA $\alpha(g)$. We now

model the preference or avoidance for certain values of $\alpha(g)$, $\tau(g)$ and $\gamma(g)$ with a set of penalty functions f_α , f_τ , f_γ which are of the general form

$$f(x) = ax^b \quad (4.1)$$

with a being a parameter responsible for the weighting of the rule and b a parameter defining the shape of the penalty function. b particularly defines how strongly deviations from a rule are punished i.e. how quickly penalty values increase when rule deviation increases.

The most simple model combining these penalties is to assume that the penalty values of all rules for a particular g are summed up

$$p(g) = f_\alpha(\alpha(g)) + f_\tau(\tau(g)) + f_\gamma(\gamma(g)) \quad (4.2)$$

and that the g associated with the lowest penalty value will be chosen for grasping.

4.2 Results

Experiments one and two were conducted in order to estimate the model parameters introduced above. They were designed as rule-conflict experiments. This means that participants were forced to reveal to which extent they prefer to satisfy one rule at the cost of the other. Experiment three served as a test of the model.

4.2.1 Experiment 1

In experiment one participants grasped rectangular blocks with a precision grip of index finger and thumb. Prior to the experiment we measured the NGA of each participant by presenting discs for grasping: In a disc the grasp angle can be chosen freely without changing force closure or distance to gravicenter. In the experiment one rectangular block was aligned with one of its cardinal axes to the participants

NGA such that it was possible to grasp it with zero deviance from perfect force closure, zero gravicenter distance and zero deviance from NGA ($\gamma = 0$, $\tau = 0$, $\alpha = 0$). Additional to this neutral block we used several blocks rotated away from the participants NGA such that participants had to decide if they follow the rotation with the digits. This would ensure good force closure but increase the deviation from their NGA. The value of τ , however, could always freely be chosen and thus played no role in this experiment. Figure 4.2 shows the data from this experiment along with the predictions of the corresponding rules. As τ played no role in this

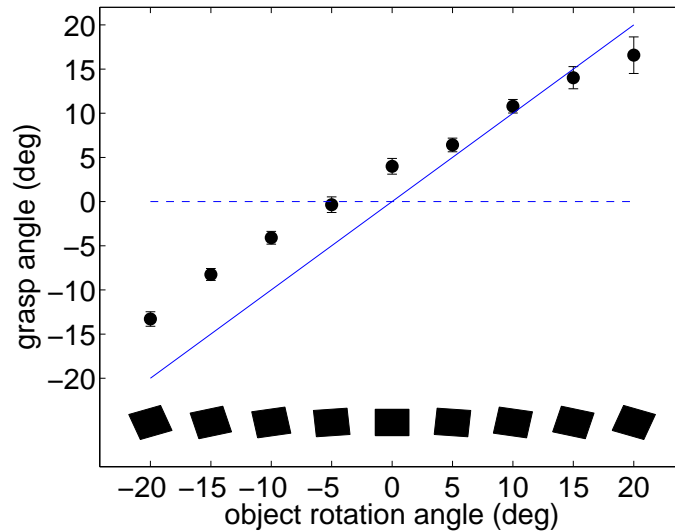


Figure 4.2: Mean realised grasp angle to the rectangular objects of experiment one. The solid line indicates the grasp angle expected for perfect force closure. The dashed line shows the grasp angle expected for no deviance from NGA. Rectangles in the bottom row schematically show the rotation of the stimuli used. Black circles show mean values of the chosen grasp angle. Errorbars are one SEM between participants.

experiment the penalty function simplifies to

$$p(g) = f_{\alpha}(\alpha(g)) + f_{\gamma}(\gamma(g)) \quad (4.3)$$

Because γ in this experiment only depended on the rotation angle (r) of the object and the value of α chosen by the grasper the penalty function in this case can also

be expressed as

$$p(\alpha, r) = f_\alpha(\alpha(g)) + f_\gamma(\alpha(g), r) \quad (4.4)$$

According to the model the grasp chosen by participants on average must represent the optimal combination of the involved rules. Any deviation of the digits from these positions would result in higher penalty values. This enables us to make an estimation of the parameters of the penalty functions involved in this experiment. We did so by using f_γ as a reference function with $a_\gamma = 1$ and $b_\gamma = 2$ and minimizing the objective function

$$c = \sum_r \left(\frac{\delta}{\delta\alpha} p(\alpha_r, r) \right)^2 \quad (4.5)$$

For the estimation we used standard software (Matlab, R2007b). As in a grip the chosen grasp axis depends on finger configuration and wrist rotation and as especially changing the latter might not be equally comfortable in clockwise and counterclockwise direction we estimated two separate penalty functions. Our results were

$$f_\alpha(\alpha) = 1.77\alpha^{1.76} \quad (4.6)$$

for the clockwise and

$$f_\alpha(\alpha) = .78\alpha^{1.9} \quad (4.7)$$

for the counterclockwise direction of rotation away from the NGA.

4.2.2 Experiment 2

In experiment two participants grasped ellipsoid shaped objects. As in experiment one we assessed the NGA of each participant by presenting disc trials in advance. We then aligned all ellipse objects with their minor axis to the participants NGA. The neutral ellipse object had its gravicenter at the intersection of the major and minor axis. Therefore it was possible to grasp it there with zero deviance from perfect force closure, zero gravicenter distance and zero deviance from NGA ($\gamma = 0$, $\tau = 0$, $\alpha = 0$). In the other ellipses the gravicenter was visibly shifted along the major ellipse axis. Participants had to decide if they follow this shift when grasping.

Following the shift would ensure a small distance to the gravicenter and thus a small value of τ . At the same time, however, due to the curved ellipse contour it would result in a larger deviance from perfect force closure and thus enlarge γ . As the ellipse was oriented to the personal NGA of the participant the value of α played no role in this experiment. Data of this experiment along with the predictions of the two rules are plotted in figure 4.3. In the data we observed that participants on

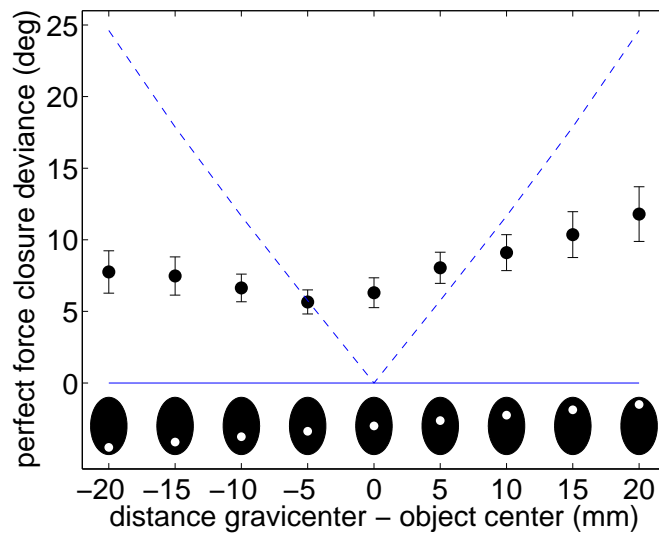


Figure 4.3: Mean realised angular deviance from perfect force closure (γ). The solid line indicates perfect force closure ($\gamma = 0$), the dashed line the deviance from perfect force closure associated with zero distance of the grasp axis to the objects gravicenter ($\tau = 0$). Ellipses in the bottom row schematically show the position of the gravicenter in the object. Black circles show mean values of the chosen grasp angle. Errorbars are one SEM between participants.

average did not realize a perfect force closure grasp even in the neutral condition. In figure 4.3 this manifested in an intercept > 0 of all the force closure deviance values. The reason for this was an undershoot in the average movement of participants. We observed a similar behavior to a lesser extent in experiment one as well. For this reason we included a linear penalty increase for longer movement distances (λ) into the model. Because in our experiments the distance was held constant and not

systematically varied the shape of the penaltyfunction i.e. a power coefficient could not be estimated for this rule.

For the estimation of the penalty functions we again used f_γ as a reference function. As all objects in experiment 2 had the same weight and because α had not to be considered the penalty function could be written as

$$p(d, k) = f_\gamma(d) + f_\tau(d, k) + f_\lambda(d) \quad (4.8)$$

In this equation d is the distance of the intersection point of grasp axis and major ellipse axis to the ellipse center. The distance of the gravicenter to the ellipse center is denoted with k . The value of γ directly depends on d . The value of τ depends on the distance between the intersection point and the ellipse barycenter. For the average rotation of the ellipse also λ can be expressed as a function of d . By minimizing

$$c = \sum_k \left(\frac{\delta}{\delta d} p(d_k, k) \right)^2 \quad (4.9)$$

We determined the penalty function of τ to be

$$f_\tau(\tau) = 5.5 \cdot 10^3 \tau^{1.8} \quad (4.10)$$

while the penalty function for movement distance amounted to

$$f_\lambda(\lambda) = 4.87\lambda \quad (4.11)$$

The penalty value for a grip calculated with the full model is thus specified as:

$$p = \gamma^2 + 1.77\alpha^{1.76} + 5.5 \cdot 10^3 \tau^{1.8} + 4.87\lambda \quad (4.12)$$

for the clockwise and

$$p = \gamma^2 + .78\alpha^{1.9} + 5.5 \cdot 10^3 \tau^{1.8} + 4.87\lambda \quad (4.13)$$

for the counterclockwise direction of α . All measured model components are specified in SI units (rad for angles, meter for distances, kilograms for object weight).

4.2.3 Experiment 3

In the third experiment we presented a set of nine complex shaped objects to our participants. Based on the estimated parameters of experiment one and two we calculated penalty values for all pairs of contact points for each object. We created model maps depicting the penalty values of all grasps for the three grasp rules and their weighted combination in a 2D configurational space (*grasp space*) which ignores the objects height.

Figure 4.4 shows the three penalty maps corresponding to the three rules of which complete penalty functions were estimated. Figure 4.5 shows a complete penalty map consisting of the sum of all penalty values including the penalty for a longer movement distance. In figure 4.6 we depict all the grasp points to each object of experiment three. Figures 4.7 and 4.8 show the complete penalty maps with and without individual grasps onto these stimuli. Because the objects were presented at the same angle for every participant the penalty map depends on the individual participants NGA (which was determined by disc trials like in experiments one and two). For the maps depicted here we used the mean NGA of the whole sample of experiment three for illustration purposes.

As a way to represent the fit of the model numerically we calculated for every participant and grasp a model quality index which is the percentage of grasps having a higher penalty value than the chosen grasp. The mean value of this quality index across all objects and participants amounted to 98.02%, the lowest value for one object being 96.97% and the highest 99.11%. We then ran a threefold test on the model in order to validate the results.

Firstly we tested the model against a random set of penalty values. To this end we calculated the predicted penalty value for every possible grasp per object and participant and then randomly permuted the assignment between realised grasp and penalty value. We created 50 random models of this type and tested the results per participant ($n = 18$) against the true model. We tested prediction quality with

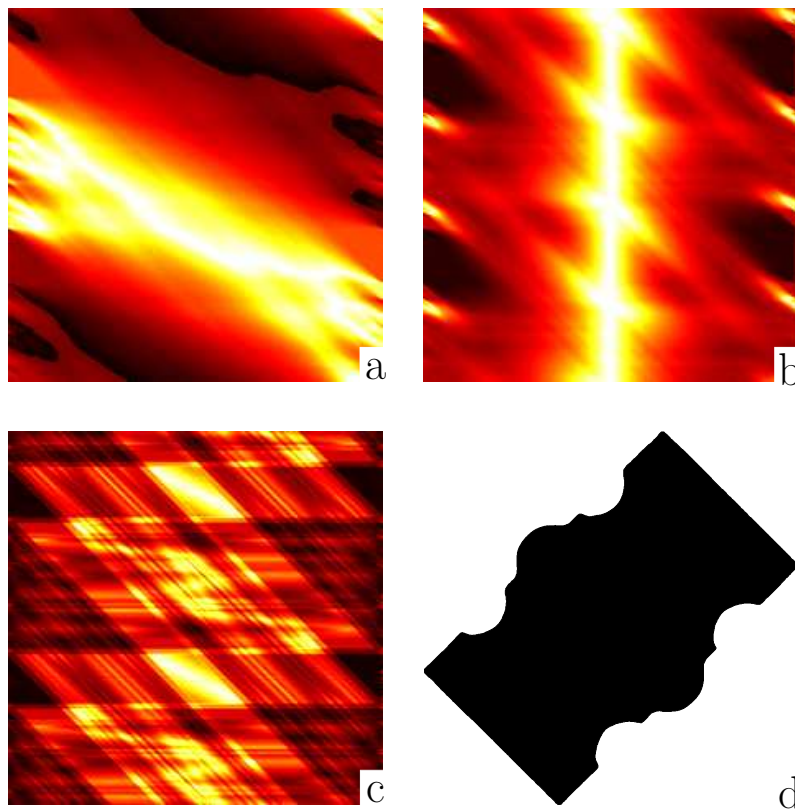


Figure 4.4: Penalty maps for one of the stimulus objects of experiment three. The y -axis depicts the arc length along the objects contour from an arbitrarily chosen start point. On this axis the contact point of the index finger is mapped. The x -axis depicts the distance between the contact points of index finger and thumb along the object contour. Every point in the map thus corresponds to one grasp consisting of a pair of contact points. The color denotes the penalty value of this grasp: low penalties are coded light while high penalty regions are dark. Color values are adapted to the penalty range of each map for clarity. *a)* Penalty map for the natural grasp angle rule. *b)* Penalty map for the torque rule. *c)* Penalty map for the force closure rule. *d)* Contour of a stimulus from experiment 3 used for calculating the penalty maps.

Wilcoxon's signed rank test. Prediction quality was significantly higher in the true model ($\bar{x} = 98.02\%$) than in the random models ($\bar{x} = 49.96\%$, $V = 171$, $p < .001$).

Secondly we tested if predictions for one stimulus object can be used for another object. This would mean that the model is not discriminative between objects but

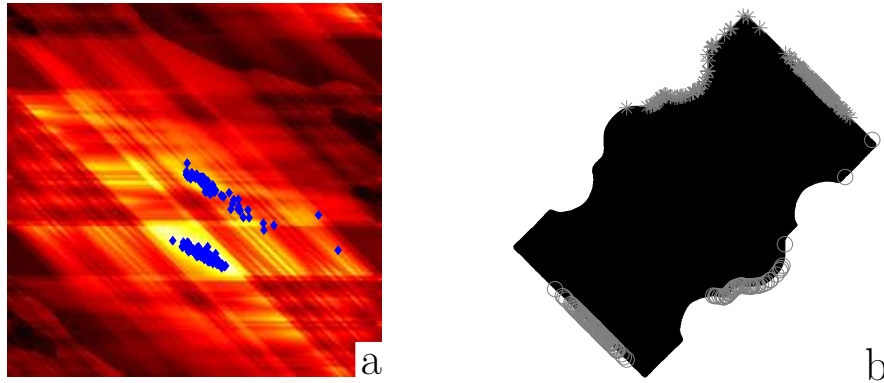


Figure 4.5: *a)* Complete penalty map consisting of the sum of the three maps shown in figure 4.4 and the additional penalty for longer distances to the starting point. Each blue diamond corresponds to one pair of contact points chosen by a participant. *b)* The same contact points plotted along the objects contour. \circ : Contact points of the thumb, $*$: contact points of the index finger.

makes some general guess valid for the whole set. We tested this by permuting the assignment between stimulus object and penalty values. Illustrative this would mean switching the penalty “map” of one object as it is e.g. depicted in figure 4.5 to another object. We recalculated the quality index for every possible object/map combination. The correct combination of object and map had a significantly higher quality index ($\bar{x} = 98.02\%$) than the control combinations ($\bar{x} = 92.7\%$, $V = 171$, $p < .001$).

Lastly we tested permutations of penalty function coefficients used in the model. To this end we used e.g. the power coefficient of the force closure rule on the torque rule and recalculated the quality index. We did this with every possible combination of coefficients also mixing between factors (*a*) and exponents (*b*). The true model combination had a significantly higher quality index ($\bar{x} = 98.02\%$) than the permuted models ($\bar{x} = 80.31\%$, $V = 171$, $p < .001$).

It should also be noted that in all three validation analyses mentioned above no single simulated model outperformed the true model.

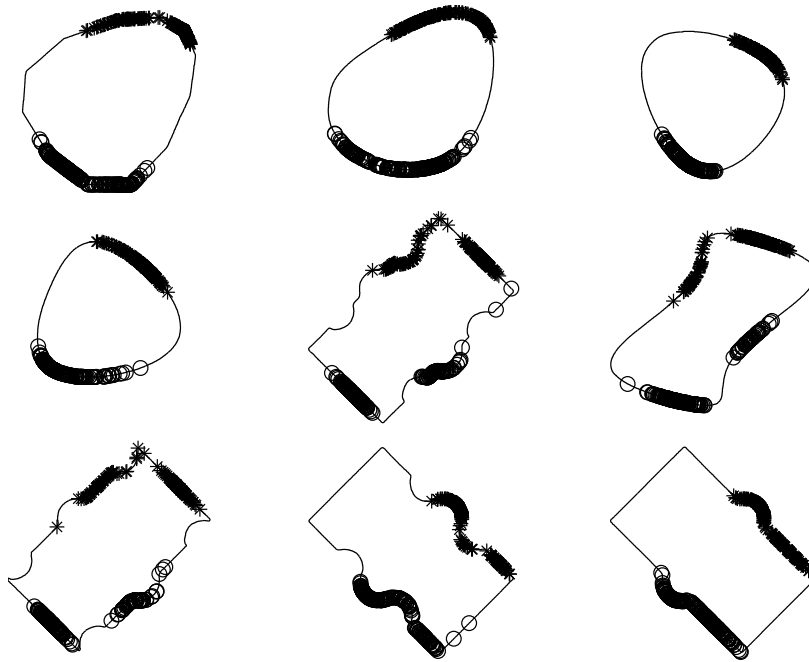


Figure 4.6: Outlines of all objects used in experiment three with the contact points chosen by participants. \circ : Contact points of the thumb, $*$: contact points of the index finger.

4.3 Discussion

We presented the first quantitative model on human grasp point selection. The model embodies four rules whose associated penalty values are summed up to a final penalty value for each possible grasp. We were able to show that the model is highly successful in predicting those points in grasp space where people actually place their grip. The output of the model can now be integrated into existing approaches for modelling human movements (Smeets & Brenner, 1999) or into control algorithms for cortically controlled prosthetic devices (Wessberg et al., 2000).

Further improvement of the model would perhaps be possible by estimating the full penalty function associated with the movement distance. Including this rule in our predictions of experiment three had a rather small effect on prediction quality (98.02% with as compared to 97.93% without it). This may well be due to the

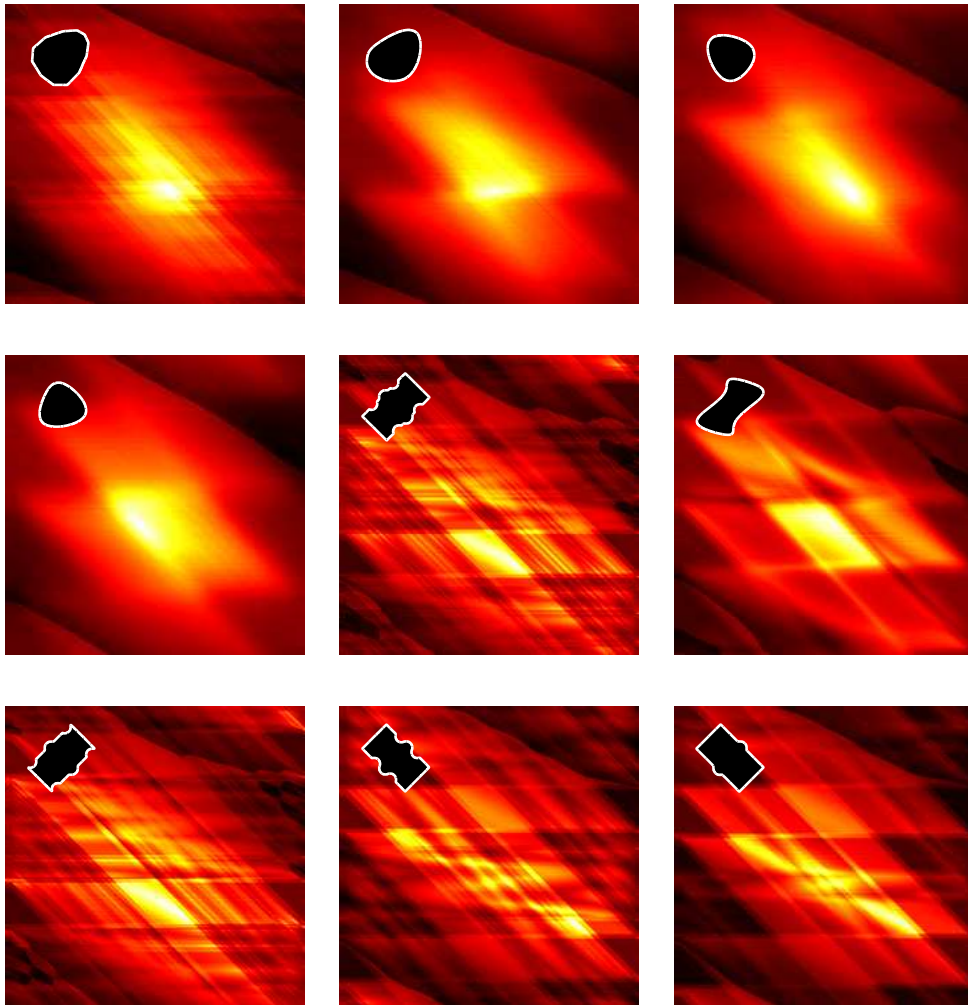


Figure 4.7: Complete penalty maps of all objects. Panels show the maps of the nine objects of experiment three without grasps. The shapes in the upper left corner of each panel show the contour of the stimulus used. Light colored regions have a low penalty value while dark regions correspond to a high penalty value in the model.

unknown shape of the function.

An improvement in terms of a model with stronger independence from the particular grasper could be made if the factors which determine the orientation of the NGA were known. In our approach this value first must be measured empirically. It would be advantageous if one would be able to predict this value for any location in the participants operating space for example from anatomical attributes of the

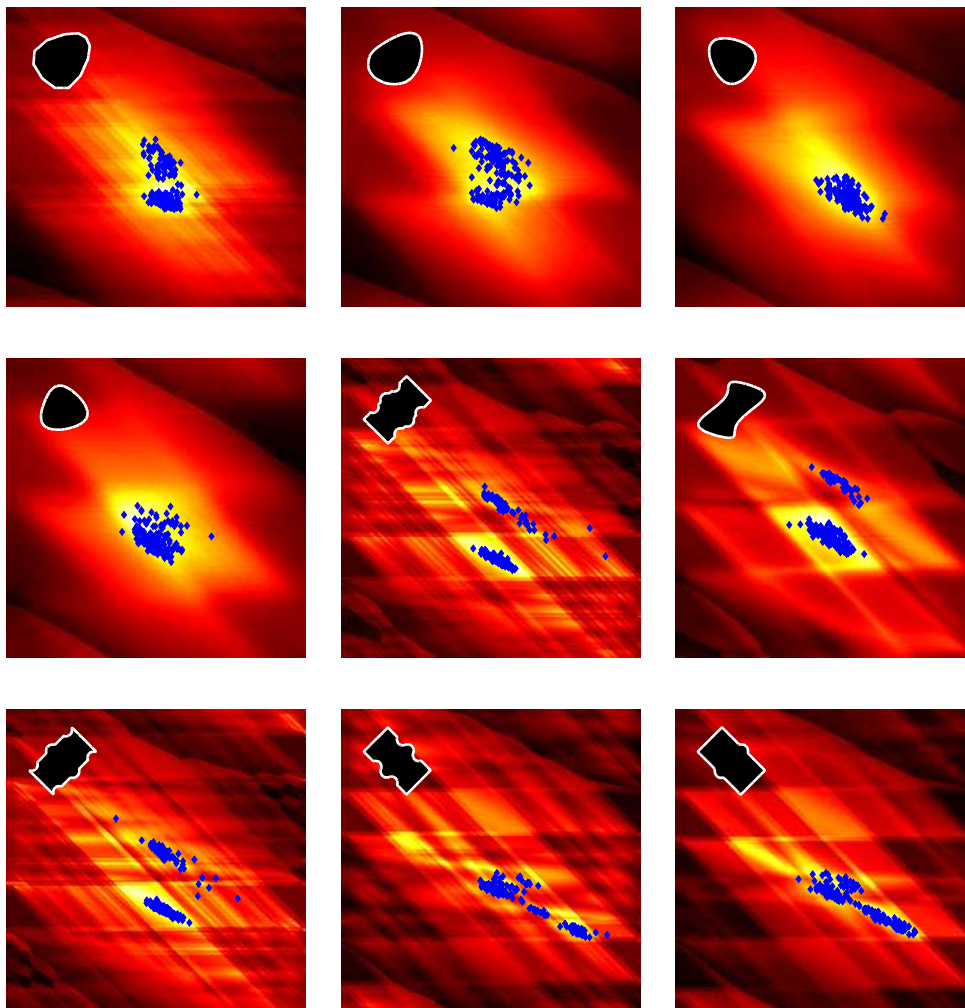


Figure 4.8: Complete penalty maps of all objects with contact points. Blue diamonds show the grasp point selections of the participants on the same penalty maps as presented in figure 4.8.

grasper like e.g. arm length.

Finally a cross validation of the shape of the penalty functions used in our model would be desirable. This shape could for example be assessed experimentally by rewarding graspers for a deviation from the rules and assessing the costs necessary to obtain a certain rule deviation.

4.4 Method

4.4.1 Participants

In experiments one, two and three we measured 17, 19 and 18 participants with 3, 5 and 5 of them being male respectively. The mean age was 24 years in all experiments. Informed consent was obtained according to the Declaration of Helsinki. Methods and procedures followed the guidelines of the Deutsche Gesellschaft für Psychologie. Participants were paid eight euro per hour.

4.4.2 Stimuli

The stimuli of all three experiments were made of black plastics material (polyoxymethylen) with a density of 1.38g/cm^3 .

In experiment one we used a disc of 2.5 cm radius and nine square blocks of 5 cm edge length. All objects had a height of 1.5 cm.

In experiment two we used a disc of 2.5 cm radius and nine ellipsoids with an extent of 10 cm along the major and 5 cm along the minor axis. Each contained a clearly visible lead cylinder of 1.5 cm radius and 0.8 cm height which was shifted between objects along the major axis of the ellipse such that the gravicenter moved from -2 to $+2$ cm in steps of 0.5 cm relative to the ellipse center. All objects of this experiment and experiment three had a height of 1 cm and a weight of 89 g.

Stimuli of experiment three were one disc of 2.5 cm radius and nine objects of complex shape. The contours of those objects are pictured in figure 4.6. All objects were 1 cm high. Their weight ranged from 38 to 56 gram.

4.4.3 Experimental setup

Participants were seated in front of a table with their head resting on a chinrest. The pod holding the stimuli was mounted at a distance of 36 cm from the chinrest and aligned in the participants' saggital plane. It could be rotated for adjusting the stimulus orientation to the individual NGA. At the right side of the subject the

starting point consisting of a small plastic knob was mounted at a distance of 36 cm from the object holder. Participants wore liquid-crystal shutter glasses (Milgram, 1987) which enabled us to obscure vision of the stimuli and the setup arrangement between trials.

4.4.4 Movement recordings and analysis

Movements of our participants were measured using an Optotrak 3020 infrared tracking system at a frequency of 200 Hz. Three infrared markers of the system were attached to the participants index finger and thumb respectively. The contact point on the fingertip of each digit was calibrated for every subject in relation to the three markers. In the experiment the contact points with the object then were obtained at the moment of object liftoff by using a speed criterion.

4.4.5 Experimental procedure

In all experiments participants were instructed to grasp the target object with a precision grip of index finger and thumb, lift the object some centimeters and carry it towards the experimenter who sat at their right side. The shutter glasses remained open for three seconds from trial onset and subjects completed the whole movement during this time interval. After the three seconds the shutter glasses closed and remained so until the start of the next trial. We used six to ten training trials which were not subjected to analysis before the main experiments. In each experiment then 25 to 30 trials with a disc object followed. In experiment one and two the experimenter then rotated the object holder according to the subjects NGA. The shutter glasses were opaque during this manipulation and participants were un-specifically told that the setup would be adjusted. Then the experiment proceeded with the experimental trials using a random sequence of the stimuli described above. Every stimulus was grasped ten times per participant.

4.4.6 Statistical analysis

We used Matlab (Matlab R2007b with Optimization Toolbox) for the estimation of the free parameters of the model. Statistical tests of the cross validation were conducted using the statistics package R (R Development Core Team, 2008).

Chapter 5

Discussion

In the remainder of this thesis I will give a summary of the results obtained by the experimental work presented in the preceding chapters. I will also discuss the implications which arise from these results and the results of related research. I will give an outlook and suggestions where future research in my opinion should be directed in order to further elucidate the questions which are still remaining, or have arisen, after this thesis. Lastly I will give an account on possible fields of application for the grasp point selection model presented in chapter 4.

The three projects presented in this thesis can thematically be organized into two main themes: Experiments of the first two projects (chapters 2 and 3) have been inspired by the two visual systems hypothesis of A. D. Milner and Goodale (1995). The experiments of the third project (chapter 4) have no strong association with this theory but deal with a general problem every model of precision grip grasping needs to solve. Therefore in the following pages I will discuss the results of the different chapters grouped by this thematical distinction.

5.1 Conclusions and outlook from chapters 2 and 3

In chapters 2 and 3 me and my collaborators used two different approaches with the common goal to test the predications of the two visual systems hypothesis of A. D. Milner and Goodale (1995).

5.1.1 Summary of the results

In chapter 2 we used the dorsal streams insensitivity to chromatic information, which is implied by the theory. We designed stimuli in a way that participants could only use this information in order to control their grasp movements. The critical stimuli were isoluminant with the background and had just a chromatic contrast with it. The outcome of this experiment was that humans have no problems using only chromatic information for grasping. These results we obtained from grasp data were consistent with the literature on other actions directed to or guided by isoluminant stimuli like saccades or pointing (Anderson & Yamagishi, 2000; White et al., 2006) although it was mentioned that Braun et al. (2008) found longer movement initiation latencies in smooth pursuit eye movements to isoluminant targets.

In chapter 3 we aimed at a replication and generalization of earlier results reported by Himmelbach and Karnath (2005). These authors had conducted research into an effect reported by several researchers: A. D. Milner et al. (1999, 2001, 2003); Revol et al. (2003); Rossetti et al. (2005) all had shown that in patients suffering from optic ataxia pointing or grasping accuracy can be improved by introducing a delay between target presentation and movement execution. Subsequently Himmelbach and Karnath (2005) in particular demonstrated that in pointing this improvement linearly increases with delay time. We tried to replicate these results and also wanted to know if a linear improvement with delay can be found in grasp movements as well. In our data, however, we could find no effect of delay at all in the grasp task. In pointing an improvement with longer delay times was only detected in the amplitude pointing errors of one patient (R.W.). In reviewing the

literature on the effect thoroughly we moreover discovered that the reported effect is far from being robust. Different researchers could demonstrate an improvement with delay in a variety of dependent variables but rarely in the same. Moreover some of the studies reported results on variables without applying statistical testing at all (e.g. A. D. Milner et al., 2003; Rossetti et al., 2005) or statistical significance was only reached by employing problematic one-sided testing (Himmelbach & Karnath, 2005). One could argue that a proof of existence of the effect in some patients would be enough to support the two-visual systems approach. A. D. Milner and Goodale (2006) argue like that in the second edition of their book *The visual brain in action* with respect to studies on the influence of visual illusions on actions (A. D. Milner & Goodale, 2006, p. 242). In this case it would be unnecessary that all optic ataxic patients show the effect. The minimum requirement, however, still would be that the effect is at least reliably found in the same person over and over again. By reviewing the literature, including our own results of Patient U.S. who was measured by Himmelbach and Karnath (2005) as well, we could show, however, that the effect is not even found reliably within the single patient. These circumstances make it doubtful if these data can be used as a support for the two-visual-systems hypothesis. Moreover we were also able to propose a very simple alternative explanation for the effect. We stated that improvement in such a delayed motor task could just as well arise from a longer processing time given to the individual. Longer time for processing generally leads to higher accuracy. Normally, in healthy participants, the improvement asymptotes very quickly i.e. in the millisecond range. Patients with neurological disorders, however, might need a longer time interval and thus show improvement over the range of several seconds. Also improvements might occur with respect to different variables, depending on the lesion. Our alternative explanation is adequate to account for the data and also more parsimonious than an explanation which needs two visual systems. This makes it generally preferable according to the principle of simplicity also known as Ockham's razor.

5.1.2 Implications in the context of related studies

Taken together, the results presented in chapters 2 and 3 are surely not sufficient to reject the two-visual-systems hypothesis of A. D. Milner and Goodale (1995). The color blindness of the motor system tested in chapter 2 is a rather indirect consequence of the proposed connection of the dorsal stream with the magnocellular pathway. Our results thus can also be explained by assuming a stronger mixup of magno- and parvocellular input to the dorsal stream without abandoning the two-visual-systems hypothesis as a whole. In chapter 3 we touched a more important pillar of the theory which is based to a large extent on data of patients like the ones we measured. Here we weakened the foundation of the theory by demonstrating firstly that the proposed effect isn't robust and secondly that it could be explained in a more parsimonious way, i.e. without invoking two visual systems. A possible simpler explanation, however, is no proof that the more complicated one might not nevertheless be true. There are several examples of tasks in the human body and nervous system which from an engineering point of view are solved in a rather complex way because of their evolutionary origin (the very labyrinthine path which the sympathetic innervation of the musculus dilatator pupillae takes may serve as an example from the visual sciences). Our results, however, are important pieces in an emerging picture. Several researchers recently have reported data which can hardly be brought into accordance with the A. D. Milner and Goodale (1995) two-visual-systems approach. In the domain of movements towards visual illusions in grasping, for example, which is an important cornerstone of the theory, Franz and Gegenfurtner (2008) have shown that data gathered by different researchers are in accordance—and in disagreement with the theory of A. D. Milner and Goodale (1995)—if proper, unbiased, measures are employed. Similarly Dassonville, Bridgeman, Bala, Thiem, and Sampanes (2004) showed in the case of the Roelof illusion that it is unnecessary to assume the presence of a split in the visual system in order to explain empirical findings of dissociation between perception and action. When

measuring fMRI data from an optic ataxic patient Himmelbach et al. (2009) have found no evidence that a ventral stream representation is utilized in delayed motor tasks as it was proposed by A. D. Milner et al. (2001, 2003) although the patient exhibited an improvement with delay. Most notably Pisella et al. (2006) even rocked at the foundations of the theory by challenging the most important piece of evidence, the double dissociation between optic ataxia and visual form agnosia presented by Goodale et al. (1994) in the patients D.F. and R.V. (note, however, that these authors propose an even more complex model of subdivisions in order to account for the available data).

5.1.3 Directions for further research

With regard to movements towards isoluminant stimuli in my opinion it is quite evident from our and the abovementioned studies that color contrast is sufficient to guide behavior, just as luminance contrast. Thus, at least in the context of testing the two-visual-systems hypothesis, I don't think that there is much need for further investigation.

Contrary to this, more research on movement control in optic ataxic patients should be conducted since the available results are inconclusive. In my opinion two different strategies would make sense: One is to gather a relatively large sample of patients and measure them in a delayed movement experiment all within the same setup. The current situation is characterized by several studies which used different patients, setups, and partly also different dependent variables in order to answer the same question. From none of these studies, however, data of more than two patients were reported. Statistical analyses were sometimes not at all done, if so then often at a relatively weak α level of 5%. Adjustments for multiple testing were not made. Thus I would argue that the risk of the occasional false rejection of the null hypothesis was relatively high. This problem could be overcome, and thus more meaningful data be gathered, by measuring a larger sample on the same experiment and with a more conservative level of α . As a second strategy I would endorse the

approach of Himmelbach et al. (2009) to directly measure the cortical activation of optic ataxic patients during the conduction of the delayed movement task. I believe that we can learn a lot from this kind of data as until now these direct observations of brain activity in the relevant patients are relatively rare.

I have outlined that there is an accumulating amount of studies, including the ones presented in chapter 2 and 3, which reject the two-visual-systems hypothesis as a reasonable explanation to the pattern of gathered data. In the second edition of their book, (A. D. Milner & Goodale, 2006) nevertheless see most of the contemporary research in favor of their model. The issue thus seems far from being solved and in any case the theory has been and continues to be an important guideline for much research on the localization of visuo-motor skills in the brain. In my opinion future research on visuo-motor functions should be directed a bit less on their spatial allocation. Instead a closer glance should be cast upon their correlates in temporal patterns of brain activation during motor tasks. For example, in perception it has been proposed that cortical oscillations are a fundamental principle of organization and grouping between functional units (Singer & Gray, 1995; Gray, 1999). Oscillations, (Baker, Kilner, Pinches, & Lemon, 1999) or their absence (Mann, Serman, & Kaiser, 1996), have also been found to be related to motor tasks and maybe to mediate sensori-motor feedback (Baker, 2007). I thus believe that a deeper insight on motor planning and control will be gained if the knowledge of location of functions, as it has been gathered by many studies inspired by the two-visual-systems hypothesis, in future studies will be more thoroughly combined with our knowledge on temporal patterns of activation. As Sereno, Trinath, Augath, and Logothetis (2002) point out object representation in the monkey is spread out across all cortical lobes, including areas assigned to the ventral and dorsal stream respectively. Recently Zanon, Busan, Monti, Pizzolato, and Battaglini (2010), moreover have shown that activation artificially induced by means of TMS in areas assigned to the dorsal stream spreads to ventral stream areas as well. A speculative but plausible hypothesis would thus be that areas dorsal and ventral of Forel's axis are commonly

involved in motor control and communicate different object properties by means of a network using oscillatory frequency binding.

5.2 Conclusions and outlook from the grasp point selection model

In this final section I will give an overview of the work on the grasp point selection model presented in chapter 4. After a short summary of the results I will discuss the directions further research could take. Lastly I will give an account of possible fields of application of the model, in particular in the medical and in the robotics domain.

5.2.1 Summary

In the project reported in chapter 4 the aim was a completion of existing theories on synthesizing trajectories for grasp movements. As it was outlined in the introduction (chapter 1, page 30) there are three quantitative modelling approaches to this problem in humans. These models, presented by Hoff and Arbib (1993), Smeets and Brenner (1999) and Rosenbaum et al. (2001) respectively build upon a minimum jerk approach, either in finger/arm position space (Hoff and Arbib, Smeets and Brenner) or in joint angle space (Rosenbaum et al.), for generating smooth trajectories. They differ, however, with respect to how the simultaneous movement of the two digits involved in the grip can best be described. Hoff and Arbib (1993) propose that transport of the whole hand and aperture, i.e. digit opening and closing, are controlled. Smeets and Brenner (1999) on the other hand suggest that each digit is controlled individually and that the aperture profile emerges as a consequence of their different contact points. Rosenbaum et al. (2001) propose that attainment of a stored posture is desired. All models have in common, however, that the points which are selected for grasping are constants which have to be fed into the model.

The goal of the presented contact point selection model was to derive these constants prior to a movement from properties of the object and the grasper. In combination with one of these models, which are able to generate the trajectories, it would then be possible to predict the whole movement before it takes place. Me and my collaborators conducted experiments where the most important rules of grasp point selection identified from the literature were put into conflict with each other. Then we estimated the penalty functions related with those rules in the human grasper. Lastly we combined these functions and in this way tried to predict grasp point selection in a novel set of stimuli. The model we proposed was extremely successful in predicting the human choice of points. I am thus very confident that we chose the right set of rules for the task and that the internal weighting, i.e. the estimated penalty functions, comes close to what actually happens within the motor system.

5.2.2 Limitations and further research

Despite the good fit we obtained the presented model can certainly still be improved in several ways. There are a lot of object properties which potentially could play a role in the way the rules used by us might be traded against each other. Perceived fragility for example influences grasp behavior (Savelsbergh, Steenbergen, & van der Kamp, 1996) just as object texture (McIsaac, Santello, Johnston, Zhang, & Gordon, 2009) does. Moreover, Gentilucci et al. (2001) even showed that also apparently task irrelevant object properties, like color, might influence the aperture profile of a grasp. Thus in the long run what will be needed is an exact understanding of the dimensions along which objects are represented in the brain. Starting from this it can then be assessed to which extent these dimensions play a role in the choice of contact points in precision grip grasping and the choice of trajectories selected for the transport towards them. So far, unfortunately, the knowledge about how the brains achieves object representation is still in its infancy (Hsiao & Bensmaia, 2008). However, as has been mentioned above, Sereno et al. (2002) presented evidence that in the monkey this function is spread out across all cortical lobes, including ventral

and dorsal stream areas. Knowing more about the object representation will be a useful guide for further research. To give one example: regions in the brain have been identified which are active during perception and action tasks where object size matters (Cavina-Pratesi, Goodale, & Culham, 2007). From the three discussed numerical models of trajectory generation, however, only the model of Hoff and Arbib (1993) needs size as a variable at all while the one of Smeets and Brenner (1999) works on contact locations of single digits without using object size as a controlled variable and the one of Rosenbaum et al. (2001) aims for stored postures which also do not explicitly contain grip size. Thus a more thorough knowledge on what exactly happens and is represented in these brain areas would also greatly help in establishing the neurophysiologically correct model of trajectory generation.

In order to discover the best combination of penalty functions for grasp point selection an economic approach was used in chapter 4. Economic theories are powerful tools in optimization problems. In human behavior often several objectives have to be optimized at the same time. In a grasp movement for example it can be desirable to hit the best pair of contact points while at the same time reducing movement time and avoiding some obstacles in the path. Economic theories allow us to convert the goal of fulfilling these eventually conflicting objectives into a single measure of utility by means of a utility function. By measuring the behavior of humans we can generally reveal their preferences and try to estimate the utility functions underlying their choices as it was done here in the grasp point selection model. This approach will probably be a key technology in modelling human behavior in the future. For example Trommershäuser, Maloney, and Landy (2003); Stritzke and Trommershäuser (2007) (see also Trommershäuser, Maloney, and Landy (2009); Trommershäuser (2009) for reviews) have already been very successful in relating motor behavior to an optimal outcome e.g. in terms of money (Trommershäuser et al., 2003) or game-points (Stritzke & Trommershäuser, 2007). When we ask participants to trade one “motor” variable, like e.g. movement time, against another, like e.g. accuracy, however, there is no extrinsically optimal outcome in the first

place. From an economic point of view every choice here comes from a set of equally optimal (pareto optimal) points. These are points where gain in one variable has to be “bought” by means of a loss in the other. We thus need to find out how these losses and gains are traded against each other. This trade can then be described by means of a utility function. Using these functions we can understand and simulate how the decision for a certain member of a set of options is made. As in motor control—in contrast to cognitive decision-making—the actor really seems to be able to realize economic optimality (Trommershäuser, 2009) I believe that this approach will be a fruitful technique and should be a focus of research in further studies.

5.2.3 Applications

There is much more work to do in order to arrive at an exact and physiologically plausible complete model on grasping. However, the results presented in chapter 4 can already be useful in a variety of applications.

Prostheses engineering As it has been outlined in the introduction to this thesis there is accumulating evidence that a remarkable amount of our movement competence is stored on a spinal level in what Bizzi et al. (2008) calls synergies. The higher order motoric areas of the CNS apparently are able to paste these synergies together to complete movements in order to obtain the desired outcome of an action. The grasp point selection model proposed here offers a way to artificially generate or predict the end-position of fingers when they reach the target of a grasp movement. It thus marks a level of processing which is midway between the abstract goal of a movement like e.g. “put the cookie into my mouth” and the low-level motor commands like e.g. “activate triceps while inhibiting biceps”. In patients suffering from amputation of the upper limb the knowledge of the target points humans normally chose in grasping can help designing prosthetic devices which move gracefully in a natural way. A possible way of implementation would for example utilize a small camera device which can be fitted into the frame of a pair of glasses along with

a small number of EEG electrodes attached above the motor cortex (BA4) region. When the person fixates a piece of cookie and exhibits activation in the arm region of BA4 a model of contact point selection like the one presented in this thesis in combination with a model of smooth trajectory generation (Smeets & Brenner, 1999; Hoff & Arbib, 1993) can be used to generate human-like movements in a prosthetic device in order to acquire the cookie with a natural movement at natural locations. Graceful and natural moving prostheses like these might increase the compliance in prosthesis usage. In a review of about 200 articles Biddiss and Chau (2007) report that rejection rates of electric upper limb prostheses are as high as 23% and 35% for adults and children respectively (with even higher rates for body-powered devices). Figure 5.1 pictures how such an electric prosthesis device of the upper limb which makes use of human-like trajectory planning could principally be implemented.

Early diagnosis of movement disorders Another application of a grasp point selection model or a full grasp movement synthesis model in the medical domain could be the early diagnosis of movement disorders. Pathological conditions of the motoric system at different stages of neural processing like Parkinson's disease, amyotrophic lateral sclerosis, ataxia or several motoric impairment conditions due to stroke, have a high prevalence in the population. Wenning et al. (2005) for example found a prevalence of movement disorders of 28% in a sample of 706 participants from an european (north italian, south tyrol) population. As the prevalence rises with higher age (Wenning et al., 2005) treatment of these diseases becomes more and more important in aging societies. Although for most movement disorders there still is no cure an early diagnosis helps to administer the proper medicamentous treatment early und thus can improve quality of life. Goodale et al. (1994) already used the distance which a grip has to the gravicenter of an object as a measure of grip quality in a patient study. This is a measure which is implicitly also included in the grasp point selection model presented in this thesis. Changes in grasp behavior with respect to the aperture profile (Rand, Lemay, Squire, Shimansky, & Stelmach,

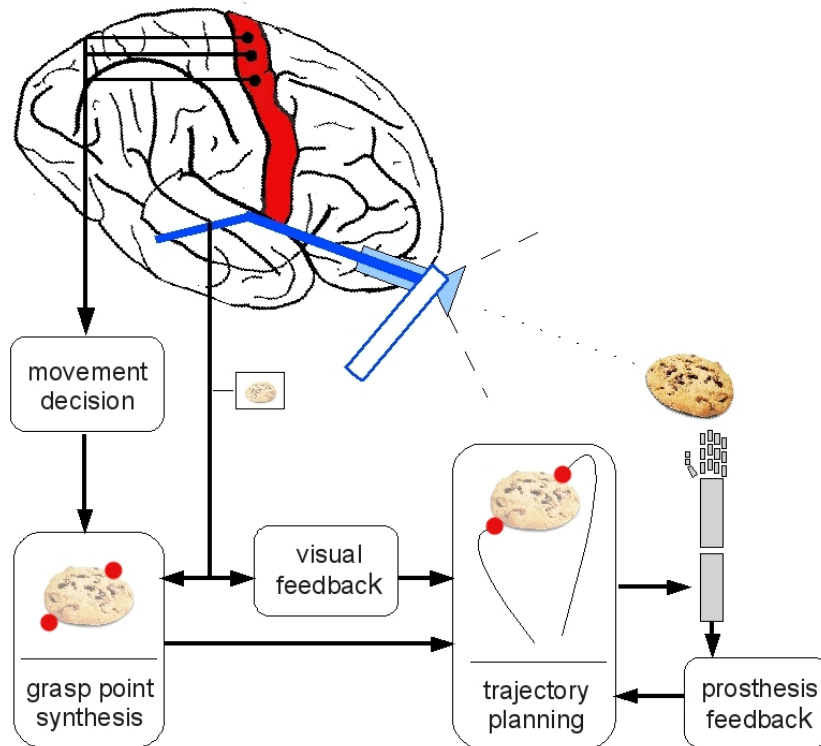


Figure 5.1: Sketch of an electrical prosthesis which is able to generate human like grasp movements. A small camera device (turquoise) which can be built into the frame of a pair of glasses (blue) captures what lies directly in front of the observer (in this case a cookie). An EEG device captures the potentials above the primary motor cortex (red). As soon as this device detects an intention to move the arm suitable grasp points towards the object currently in front of the observer are synthesized by means of a model like the one presented here which uses the transmitted camera image (frame with small cookie). A trajectory can then be planned with algorithms based on models like those of Hoff and Arbib (1993) or Smeets and Brenner (1999). In the initial state a representation of the current position of the prosthesis which is available from the prosthesis' feedback can be used for trajectory planning. As soon as the prosthesis is inside the field of vision visual feedback from the camera can be used for a better estimate of the difference between current prosthesis position and the desired end-state.

2010) or force control (Santello, Muratori, & Gordon, 2004) in Parkinson's disease have already been demonstrated as well. It seems plausible that due to pathological conditions also the penalty functions associated with grasp point selection might change. Patients with limb weakness for example might place a stronger emphasis on the torque rule on the cost of the natural grasp angle rule. In this case they would "buy" a lesser amount of necessary grip force on the cost of less grip comfort. Subtle changes like these might not be seen behaviorally as the general ability of grasping may still be intact. It could, however, be a way to assess early stages of a beginning disorder.

Robotic technology Robotic technology is another field where the grasp point selection model could find useful appliances. Robots are already an indispensable part of industrial production. They are, however, also on their way to play an important role in our everyday life. According to an overview of Tapus, Mataric, and Scassellati (2007) robots are about to assist us for example in the care of elderly people which may become more and more important in aging societies. They can also be used for rehabilitation training of patients with physical disabilities. Of course it is generally very debatable if humanoid robots should replace humans in medical care tasks like these which principally could also be done by human beings. There is, however, evidence that there are applications where it may indeed be preferable to use robots. Arehart-Treichel (2010) for example report preliminary results that children suffering from autistic spectrum disorder (ASD) might profit from interacting with robots. Children with ASD have difficulties engaging in interactions with other children and adults and often are handicapped in the development of social and motor skills. Arehart-Treichel (2010) report from promising first attempts of treating these children by letting them interact with humanoid robots (see also Tapus et al., 2007 for a short outline on some earlier studies about this topic). With respect to all of these applications it is desirable to make robots move more naturally. This can be done, amongst other things, by employing natural models of (hand)

movements. Glasauer, M, Basili, Knoll, and Brandt (2010) for example examined situations where an object has to be handed over between object and robot. They showed that humans perform better in this task if they interact with robots which mimic human movement characteristics (in this case a minimum-jerk trajectory). In the special case of autistic children I would hypothesize that a further benefit of more human-like movements will be a better generalization of social skills acquired in robot interaction to real human attachment figures.

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Danksagung

An dieser Stelle möchte ich mich ganz herzlich bei allen Menschen bedanken, die zur Entstehung dieser Dissertation beigetragen haben. Ein besonderer Dank geht an meinen Doktorvater, Prof. Volker Franz der mich seit nunmehr 7 Jahren stetig in meinen wissenschaftlichen Ambitionen unterstützt, dem ich ausserdem eine Menge wertvollster Methodenkenntnisse sowie spannende Kooperationen mit dem Labor von Prof. Jeroen Smeets und Dr. Eli Brenner sowie dem von Prof. Hans-Otto Karnath verdanke. Grosser Dank geht ebenso an den Zweitgutachter dieser Arbeit, Prof. Karl Gegenfurtner, der mich trotz meiner häufiger Unentschlossenheit und Zweifeln ebenfalls seit Jahren mit bewundernswerter Geduld unterstützt und fördert und ohne den diese Arbeit bis auf den heutigen Tag (, bitte hier Datum von heute einsetzen) nicht abgegeben worden wäre.

Besonders hervorheben möchte ich an dieser Stelle auch die Leistung aller meiner bisherigen Bürogenossen, allen voran Lukas, Owino und Matteo nicht an meiner Ungeduld und meinen Launen zu verzweifeln sowie mich immer wieder motiviert und mir geholfen zu haben.

Besonderen Verdienst am Zustandekommen dieser Arbeit hat auch Constanze Hesse von der ich mir eine Menge Code geklaut und Überlebensstrategien in Sachen Dissertations-Unlust abgesehen habe.

Bei Dr. Marc Himmelbach und Prof. Hans Otto Karnath bedanke ich mich ganz herzlich für die gute Aufnahme und Betreuung an der Uniklinik Tübingen im Rahmen des in Kapitel 3 vorgestellten Projektes zu Zeige- und Greifbewegungen bei optischer Ataxie. Prof. Laurence T. Maloney von der New York University hat mir viele wertvolle Denkanstösse gegeben, die mir eine unschätzbare Hilfe bei der Anwendung ökonomischer Techniken auf die Modellierung menschlicher Bewegungsplanung waren. Ausserdem ist er ein sehr gebildeter und angenehmer Begleiter beim Mittagessen!

Mein Dank geht auch an Alexander Schütz für jegliche kompetente Beratung in

wissenschaftlichen und technischen Fragen, für das Durchlesen meiner Entwürfe und vor allem dafür, dass er es immer wieder schafft mich auf den Boden der Tatsachen zurück zu holen (bis jetzt jedenfalls).

Hervorzuheben ist auch der enorme Beitrag den Walter Kirchner, der Daniel Düsentrieb des Labs, und unsere hauseigene Werkstatt an meinen Experimenten hatte.

Ohne zwei weitere Personen wäre diese Arbeit ebenfalls nie zustande gekommen. Deswegen möchte ich mich an dieser Stelle sehr bei meinen Eltern bedanken, die mich schon seit jeher in allem gefördert haben was sich mein manchmal wechselhafter Wille zum Ziel gesetzt hat.

Für ihre liebevolle Unterstützung möchte ich mich zum Schluß bei Jessica bedanken, die wirklich unglaublich geduldig mit mir gewesen ist und mit mir in ihren Ferien zahlreiche Nachtschichten gemacht hat um meine Motivation hoch zu halten.

Ich erkläre: Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angegeben habe. Alle Textstellen, die wörtlich oder sinngemäss aus veröffentlichten Schriften entnommen sind, und alle Angaben, die auf mündlichen Auskünften beruhen, sind als solche kenntlich gemacht. Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze wissenschaftlicher Praxis, wie sie in der "Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis" niedergelegt sind, eingehalten.

Gießen, 6. September 2010

Urs Kleinholdermann