The use of visual information when grasping objects

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

Justus–Liebig–Universität Gießen

Fachbereich 06
Psychologie und Sportwissenschaften
Otto–Behaghel–Straße 10F
35394 Gießen

vorgelegt am 23. Januar 2008
von
Constanze Hesse
geboren am 11. Dezember 1980
in Freiberg

Dekan
Prof. Dr. Joachim C. Brunstein

1. Gutachter und Betreuer
PD Dr. Volker Franz

2. Gutachter
Prof. Karl R. Gegenfurtner, PhD

Zusammenfassung

Ziel dieser Dissertation ist es, die Nutzung visueller Information bei der Planung, Ausführung und Kontrolle von Greifbewegungen zu untersuchen. Insbesondere geht es um die Frage, wie eine Veränderung der zugrunde liegenden visuellen Information sich auf die kinematischen Parameter einer Greifbewegung auswirkt. Damit geht die Arbeit über die Untersuchung der rein motorischen Aspekte der Bewegung hinaus und nutzt die Greifbewegung, um das Wissen über die neuronalen Mechanismen der visuellen Wahrnehmung und deren Zusammenhang zu zielgerichteten Handlungen zu erweitern.

Im Einzelnen wurden im Rahmen dieser Dissertation drei Serien von Experimenten durchgeführt. Im ersten Projekt der Arbeit wurde die Auswirkung einer Zeitverzögerung zwischen der visuellen Darbietung eines Objekts und der Bewegungsinitiierung untersucht. Ausgangspunkt dieser Studie ist die Zwei-Pfade-Theorie von Goodale und Milner (1995), welche dem dorsalen und ventralen Strom unterschiedliche Gedächtnisspannen zuschreibt. Während Informationen im ventralen Pfad längerfristig gespeichert werden, wird angenommen, dass der dorsale Pfad ausschließlich in Echtzeit arbeitet (Goodale et al., 2003, 2005). Entsprechend des "real-time view of action" ist für die Beteiligung des dorsalen Stroms an der Bewegungsausführung entscheidend, ob das Objekt während der Bewegungsinitiierung sichtbar ist. Ist dahingegen das Zielobjekt während der Bewegungsinitiierung nicht sichtbar, wird bei der Handlungsausführung auf die im ventralen Pfad längerfristig gespeicherte Repräsentation zurückgegriffen. Insgesamt fanden sich in den Experimenten keine Belege für einen Wechsel der genutzten Repräsentation in Abhängigkeit von der Objektsichtbarkeit während der Bewegungsinitiierung. Eher sprechen die Ergebnisse für einen exponentiellen Verfall der visuomotorischen Information, der zu den beobachteten Veränderungen in der Bewegungskinematik führt. Damit stehen unsere Ergebnisse zum Greifen nach Zeitverzögerung in sehr guter Übereinstimmung zu den Ergebnissen der Gedächtnisforschung in der Wahrnehmung, die ebenfalls von einem exponentiellen Zerfall der Gedächtnisspur ausgehen, widersprechen jedoch den Annahmen des "real–time view of action".

In der zweiten Studie wurde gezielt geprüft, ob Greifbewegungen, auch wenn sie unter voller Sicht geplant und ausgeführt werden, durch die vorausgehende Präsentation eines visuellen Reizes beeinflusst werden können. Grundlage dieser Untersuchung ist eine weitere Annahme des "real-time view of action", die davon ausgeht, dass Bewegungen zu sichtbaren Objekten stets in Echtzeit geplant und ausgeführt werden und damit metrisch korrekt und unbeeinflusst von vorausgehenden visuellen Erfahrungen sind. Die Ergebnisse des zweiten Projekts zeigen jedoch, dass auch visuell geleitete Bewegungen von vorausgehenden Wahrnehmungen beeinflusst sind. Dies legt nahe, dass die Bewegungsplanung bereits beginnt, bevor tatsächlich eine Handlung verlangt wird. Dieser Befund steht erneut im Widerspruch zum "real-time view of action".

In der dritten Experimentalserie wurde untersucht, wie und in welchem Zeitver-

lauf visuelle Informationen zur Korrektur von Greifbewegungen genutzt werden. Dazu wurde die Objektgröße eines Zielobjektes zu verschiedenen Zeitpunkten während der Bewegung verändert. Weiterhin wurde geprüft, inwieweit die Sichtbarkeit der Hand während dieser Korrekturen von Bedeutung ist, um auf zugrunde liegende Feedbackmechanismen schließen zu können. Insgesamt implizieren die Ergebnisse, dass kleinere Veränderungen der Objektgröße zu Bewegungsbeginn schnell und kontinuierlich in den Bewegungsablauf integriert werden können. Da auch ohne Sichtbarkeit der Hand während der Bewegung Korrekturen in Richtung der neuen Objektgröße erfolgten, scheinen klassische Feedbackmechanismen nicht unbedingt nötig zu sein, um eine effiziente Anpassung der Bewegung zu gewährleisten. Stattdessen scheint es möglich, allein mittels kontinuierlicher (feedforward) Planung effiziente Korrekturen der Bewegung durchzuführen.

Zusammenfassend hat diese Doktorarbeit gezeigt, dass die Steuerung des motorischen Systems auf einer sehr flexiblen Verarbeitung visueller Information beruht, die in vielen Aspekten denen der Wahrnehmung gleicht. Die Ergebnisse sprechen daher dafür, dass Wahrnehmung und Handlung von ähnlichen neuronalen und funktionalen Prozessen generiert werden. Dies wird auch von Studien nahegelegt, die mittels bildgebender Verfahren zeigen, dass ähnliche kortikale Aktivierung während Wahrnehmungs- und Handlungsaufgaben auftritt (e.g., Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997; Faillenot, Decety, & Jeannerod, 1999).

Abstract

The aim of this thesis is to examine the role of visual information for the planning, execution and control of grasping movements. In several behavioral studies I investigated the changes in grasping kinematics resulting from a change of the underlying visual information. Thus, the intention was, beyond understanding the processes of grasping in more detail, to use grasping movements as a tool to learn about the processes of perception.

In the first project, it was tested in which way the amount of visual information influences the execution of goal–directed grasping movements. Theoretical background of this study is the proposition of the real–time view of action (Westwood & Goodale, 2003; Westwood, Heath, & Roy, 2003; Goodale, Westwood, & Milner, 2003; Goodale, Kroliczak, & Westwood, 2005) stating that movements directed to visible and remembered objects are controlled by different processing mechanisms (dorsal vs. ventral pathway). We tested this prediction by examining grasping movements executed under full vision and after three different delay durations. Results indicate that changes of grasping kinematics are due to an exponential decay of visuomotor information and not due to a change of the representation used, therewith contradicting the real–time view of action.

The second study dealt with another prediction of the real–time view of action. It has been argued that movements to visible targets are calculated in real–time and are not influenced by perceptual memory or any earlier movement programming (e.g., Cant, Westwood, Valyear, & Goodale, 2005; Garofeanu, Kroliczak, Goodale, & Humphrey, 2004). This hypothesis was tested by visually presenting a distractor object of a certain orientation and measuring grip orientation when grasping a target object subsequently. Results showed that the kinematics of visually guided grasping movements are affected by the properties of the previously shown distractor object. The study provides evidence that perception and memory are involved in the execution of visually guided movements. This finding also contradicts the real–time view of action.

The third project was concerned with the effects of size–perturbations on the grasping movement. The aim was to investigate the adjustment of the grip under different conditions. Results indicate that vision of the hand is not necessary to correct the grip successfully during movement execution. Consequently, these experiments suggest that feed–forward mechanisms play a major role in adjusting a planned motor program.

Taken together, the findings obtained in all projects provide evidence that action and perception interact strongly. This is also supported by recent neuroimaging studies showing that the cortical activation during perception and action tasks largely overlaps (e.g., Faillenot et al., 1997, 1999). Furthermore, our experiments show how grasping movements are influenced by different object properties and task demands.

Contents

Chapter 1

General Introduction

Many human actions are directed toward objects. To reach out and grasp something is an exemplary movement for such a goal–directed action. This apparently very simple movement has kept hundreds of scientists busy since the beginning of its systematic investigation. The mechanisms underlying a grasping movement have turned out to be very complex requiring multiple visuomotor transformations mapping the visual information about physical characteristics of the object into motor commands (e.g., Jeannerod, 1999; Castiello, 2005).

It is relatively obvious that for the execution of more complex actions, such as grasping, visual and motor processes have to interact strongly. Movement programming is largely determined by the visual perception of the object to be grasped. Based on this visual information we decide how we pick the object up, whether we use one or two hands and how we orientate the hand in space. The accuracy of a grasping movement is therefore very closely related to the accuracy of the underlying perceptual processes (Rosenbaum, 1991). Thus, motor control and visual perception cannot be regarded as independent processes. This means that studying grasping movements is always related to the study of vision and allows insights in motor as well as perceptual functions and their coupling. In the following, the relevant aspects of the visual as well as the motor system when executing a grasping movement are briefly summarized.

1.1 Two visual systems

1.1.1 "WHAT" versus "WHERE"

Since the late 1960s, a number of different functional dichotomies of the visual system have been proposed (e.g., Trevarthen, 1968; Schneider, 1969; Held, 1970; Ungerleider & Mishkin, 1982). One of the first distinctions between two streams of visual information was suggested by Trevarthen (1968) who proposed that vision of space and vision of object identity may be subserved by anatomically distinct brain mechanisms (in particular the more ancient subcortical visual system). According to Trevarthen (1968) vision involves two parallel processes: (a) the ambient system (mediated by superior colliculus), determining space at large around the body and guiding whole–body movements and locomotion, and (b) the focal system (mediated by geniculostriate system) examining details in small areas of space and guiding fine motor acts. More influential at this time, however, was the distinction put forward by Schneider (1969) who argued that the retinal projection to the superior colliculus enables organisms to localize a stimulus in space, while the geniculostriate system allows them to identify the stimulus. Although the two visual system hypothesis as proposed by Schneider (1969) is no longer as popular, the dichotomy distinguishing between object identification (*WHAT*) and object localization (*WHERE*) persisted in visual neuroscience and was modernized by Ungerleider and Mishkin (1982) assigning the pathways to cortical areas. According to this very influential theory, based on studies of the macaque monkey, the division between "what" and "where" was mapped on to two diverging streams of output from the primary visual cortex (V1): one progressing ventrally to the inferotemporal cortex, and the other one dorsally to the posterior parietal cortex (cf. Figure 1.1). In short, it was proposed that the dorsal pathway is responsible for extracting information about the spatial layout of the environment and motion, whereas the ventral pathway extracts information about the identity of objects such as color, texture and shape.

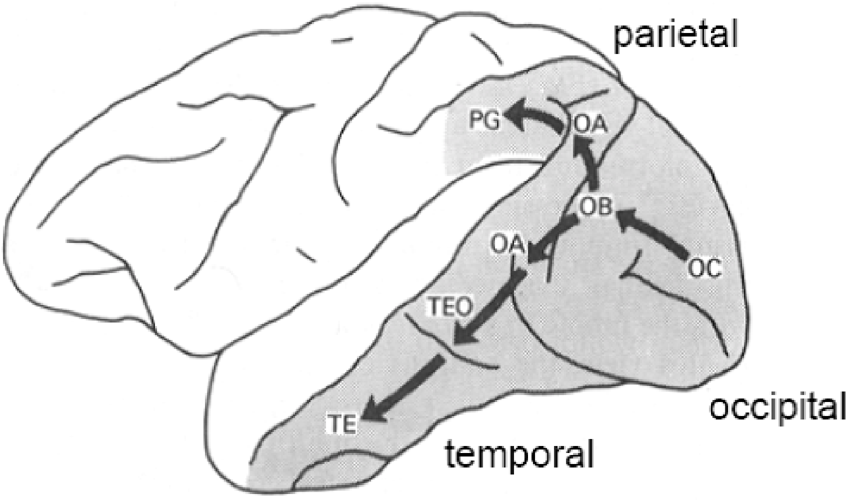


Figure 1.1: *Schematic drawing of the two streams of visual processing in the primate cerebral cortex as proposed by Ungerleider and Mishkin (1982). The arrows represent the two visual pathways, each beginning in the primary visual cortex, diverging in the prestriate cortex (OB and OA) and then going ventrally into the inferior temporal cortex (TEO and TE) or dorsally into the inferior parietal cortex (PG). Reprinted from Mishkin, Ungerleider, & Macko (1983).*

The main evidence for this dichotomy came from behavioral experiments in which the visual discrimination ability of monkeys with lesions in the different cortical areas were compared. Lesions of the inferotemporal cortex (interruption of the ventral stream) impaired the animals' ability to visually discriminate or recognize objects whereas the perception of spatial relations was unimpaired. Conversely, animals with lesions of the posterior parietal cortex (interruption of the dorsal stream) were unable to spatially discriminate between objects, while they could still recognize and identify objects correctly (cf. Figure 1.2).

On the basis of the distinction of Ungerleider and Mishkin (1982) it was proposed

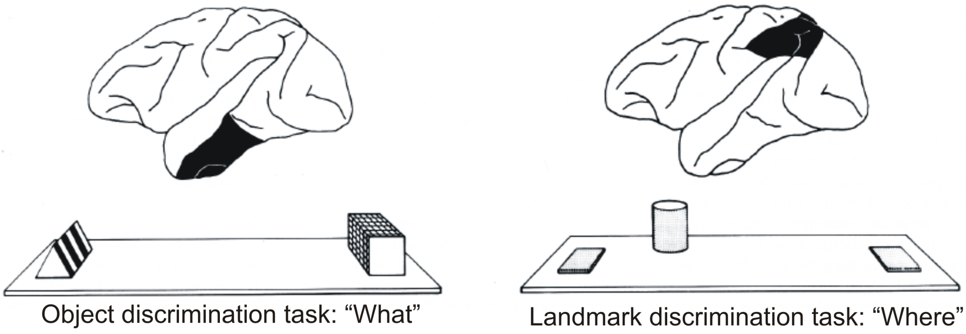


Figure 1.2: *Schematic drawing of the object discrimination task and the landmark discrimination task. In the object discrimination task the monkey is trained to choose a particular object which varied its position from trial to trial. In the landmark discrimination task the monkey is rewarded for choosing the plaque closer to the cylinder. The black colored areas show the brain lesion which impaired the performance most in the given task. Reprinted from Mishkin, Ungerleider, & Macko (1983).*

by Livingstone and Hubel (1988) that the two streams can be traced back to the two main cytological subdivisions of retinal ganglion cells terminating either in the parvocellular layers or in the magnocellular layers of the lateral geniculate nucleus (LGN). To give a short description, it was shown that parvo cells are color–coded and have high spatial resolution. Thus, the parvo cells were assumed to transmit information about color and form along a ventral stream to area V4 and finally in the temporal lobe, where object recognition is believed to takes place. In contrast, the magno cells are color–blind, but have high contrast sensitivity and temporal resolution. Thus, these cells were assumed to transmit information along the dorsal pathway to area MT and to parietal lobe areas which are concerned with spatial localization and movement. Although magno and parvo cellular processing remains relatively segregated until the level of V1, there is recent evidence that the separation between magno and parvo information in higher visual areas than V1 is not as distinct as initially suggested (for reviews see Schiller & Logothetis, 1990; Merigan & Maunsell, 1993; Gegenfurtner & Hawken, 1996; Callaway, 2005). It rather seems to be the case that dorsal and ventral steams each receive inputs from both magno and parvo pathways.

1.1.2 "WHAT" versus "HOW"

An influential alternative theory to the above discussed "what" and "where" distinction was proposed by Milner and Goodale (1995). They argue that the dorsal and the ventral pathway differ in a much more fundamental way than suggested so far. According to the Milner and Goodale (1995) theory the pathway in which visual information is processed depends on the intended purpose: the ventral pathway is mainly involved in the identification and recognition of objects as well as in the processing of their spatial layout, whereas the dorsal pathway is responsible for processing visual information for the control of actions. Therefore, Milner and Goodale (1995) ascribe all functions of vision which were attributed to different pathways by earlier approaches, e.g., Ungerleider and Mishkin (1982), to the ventral pathway while the dorsal pathway is dedicated to the moment by moment control of movements. In other words, the dichotomy is based on the way in which information is transformed in different output purposes ("vision for perception" vs. "vision for action").

To suit these different purposes the representations generated in the different pathways are also assumed to have different properties. The representations created in the ventral pathway form the basis for our conscious experience of the visual world. In contrast, representations of the dorsal stream which are assumed to act in real–time and enable us to make fast and effective movements are unconscious. Furthermore, it is argued that both streams process information on different time scales. In order to identify and later recognize objects, viewpoint independent information must be stored over a long time in the ventral stream. Therefore, the properties of objects are encoded relative to other objects in the environment (allocentric frame of reference). In contrast, for acting on objects their spatial position relative to the body needs to be taken into account (egocentric frame of reference). Given that the relative positions of observer and target object can change quickly, the egocentric coordinates of the object's position are computed every time an action is required de novo. Therefore, the visuomotor system is expected to have only a very short "memory" meaning that the egocentric coordinates of the object's position are available for only a few seconds.

The main evidence for the distinction of the visual pathways as proposed by Milner and Goodale (1995) comes from patient studies showing that brain damage can have separate effects on conscious perception and on the visual control of movements. The theory was then further sustained by studies demonstrating that perception and action can also be dissociated in healthy subjects using visual size illusions such as the Ebbinghaus illusion (e.g., Aglioti, DeSouza, & Goodale, 1995). However, there are also some recent studies which put the validity of the evidence in favor of the "what" versus "how" distinction into question (e.g., Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Franz, 2001; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999; van Donkelaar, 1999; Dassonville & Bala, 2004). In the following the evidence put forward as support of the theory as well as the proposed alternative explanations of these findings are shortly summarized.

Patient studies Evidence for the dissociation between different modes of processing comes mainly from clinical cases with cortical lesions. In short, there are patients who are able to accurately reach and grasp an object but cannot identify it (visual form agnosia) and patients who show an inability to reach for and grasp objects appropriately despite they are able to identify them correctly (optic ataxia). Thus, whether the same attribute of an object (e.g., its size) can be correctly processed or not, seems to depend on which processing mode is requested from the patient.

Visual form agnosia: The most extensively tested patient with visual form agnosia is patient D.F. suffering from a brain damage from carbon monoxide poisoning (Milner et al., 1991). While she has relatively normal low–level visual functions her ability to recognize and discriminate even simple geometric forms is severely impaired. Her spared abilities to use visual information were examined in a series of experimental studies demonstrating the dissociation between perceptual report and visuomotor control in many different ways (e.g., Milner et al., 1991; Goodale, Milner, Jakobson, & Carey, 1991; Goodale, Jakobson, Milner, Benson, & Hietanen, 1994; Carey, Harvey, & Milner, 1996; Murphy, Racicot, & Goodale, 1996). For example Goodale et al. (1991) showed that D.F. was not able to report the orientation of an oriented slot, neither verbally nor manually, although she had no problems to insert a card in the correct orientation in the same slot (Figure 1.3). Similar dissociations between perceptual report and visuomotor control were also observed in D.F. when she was asked to deal with the intrinsic properties of objects such as their size and shape. Thus, she adjusted her grip appropriately to blocks of different sizes that she could not distinguish perceptually. Like in normal subjects her grip size was related linearly to the width of the target object (Goodale et al., 1991). However, when she was asked to use her finger and thumb to make a perceptual judgment of the object's width her responses were very variable and unrelated to the actual stimulus dimensions.

Temporal as well as spatial limits on D.F.'s ability to guide her motor behavior visually have also been reported. After showing her a rectangular target object D.F. was asked to wait for either 2 or 30 seconds with her eyes closed, before she was allowed to reach out and to pantomime the grasp of the object (Goodale, Jakobson, & Keillor, 1994). Whereas healthy subjects continue to scale their hand opening for object size when pantomiming grip formation after a delay, D.F. was not able to adjust her grip to the object size shown before (Figure 1.4). All these findings suggest that the lesion of patient D.F., due to the anoxia, is mainly located in the ventral stream while the dorsal stream remained intact. A structural magnetic resonance imaging (MRI) scan carried out one year after the carbon monoxide poisoning of D.F. showed, however, that the brain damage was not clearly localized (Milner et al., 1991). A concentrated region of bilateral cortical damage was found in the lateral

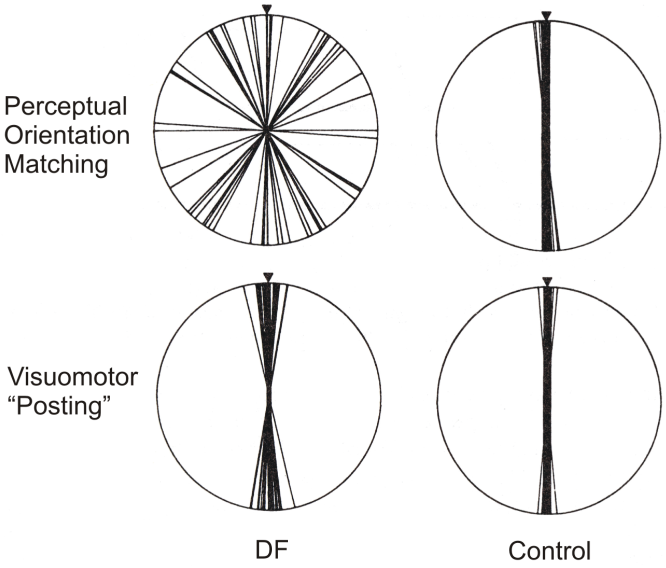


Figure 1.3: *The polar plots illustrate the orientation of a hand–held card in a perceptual task and in an action task for patient D.F. and an age–matched control subject. In the perceptual task the card had to be adjusted to the orientation of the slot presented in front of the subjects. In the action task the card had to be inserted in the presented slot. The correct orientation was normalized to vertical. Reprinted from Goodale et al. (1995).*

prestriate cortex, mainly in areas 18 and 19 (Milner et al., 1991) which are assumed to be part of the human homologue of the ventral stream. The primary visual cortex, which provides the input for the dorsal and the ventral stream was found to be largely intact suggesting that the dorsal stream still can receive cortical visual input. In addition, there was no evidence that D.F.'s tectothalamic pathways to MT or other dorsal stream areas are damaged which is in support of the interpretation of Milner and Goodale. The idea of two independently working visual systems was further strengthened by patients showing the reverse pattern of deficits than D.F..

Optic ataxia: Patients with optic ataxia following damage of the posterior parietal cortex (dorsal stream) show the inability to reach for and grasp objects appropriately despite their ability to identify them. When optic ataxic patients are asked to pick

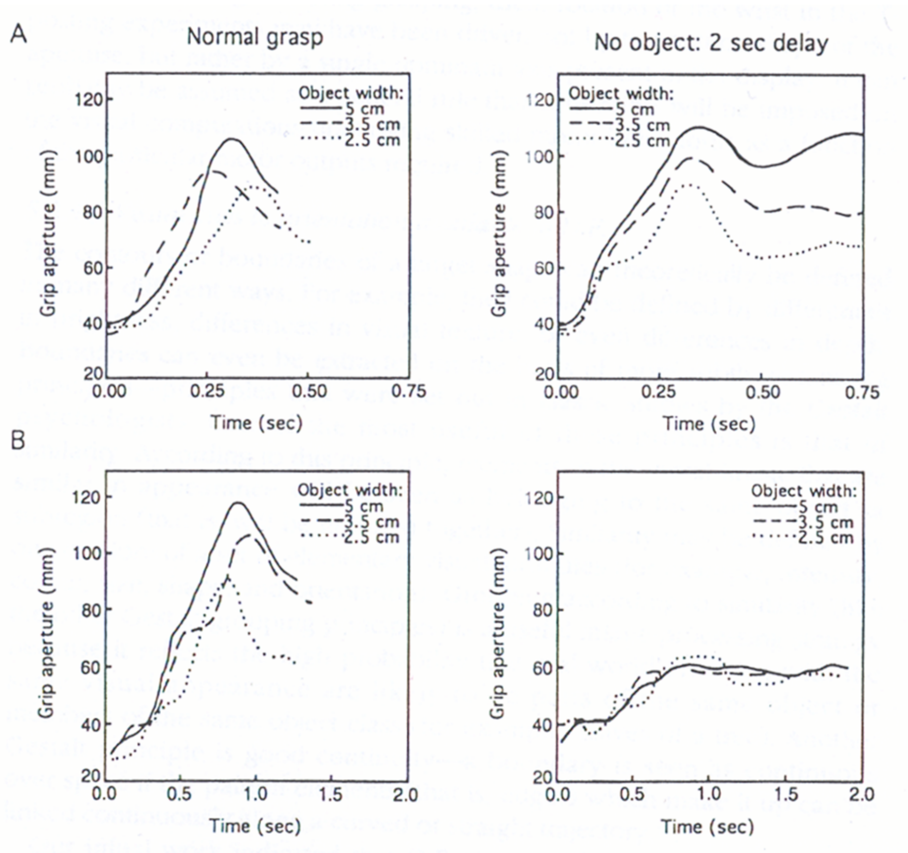


Figure 1.4: *Graphs show the aperture profiles of (A) a normal subject and (B) patient D.F. when grasping objects of different sizes either immediately or after a delay of 2 s. Whereas the normal subject continues to scale the grip to the size of the object, no such scaling of the grasp was found for patient D.F. after the delay. Reprinted from Milner and Goodale (1995).*

up objects, they are not able to adjust their grip to the shape and the size of the object despite their perceptual estimate of the object's properties remained quite accurate (e.g., Perenin & Vighetto, 1988; Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, Decety, & Michel, 1994). In a study of Goodale, Meenan, et al. (1994) the performance of D.F. when grasping an object was directly compared with the performance of a patient suffering from optic ataxia (R.V.). Caused by strokes, patient R.V. has large bilateral lesions of the occipitoparietal cortex which is assumed to be part of the dorsal stream. Whereas D.F. selected similar grasp lines as the healthy control subjects, passing approximately through the center of mass of the object, R.V. chose grasp points resulting in an unstable grip of the object (Figure 1.5). This finding is in line with the Milner and Goodale interpretation that patient R.V. suffers from a damage in the dorsal stream while still retaining an intact ventral stream.

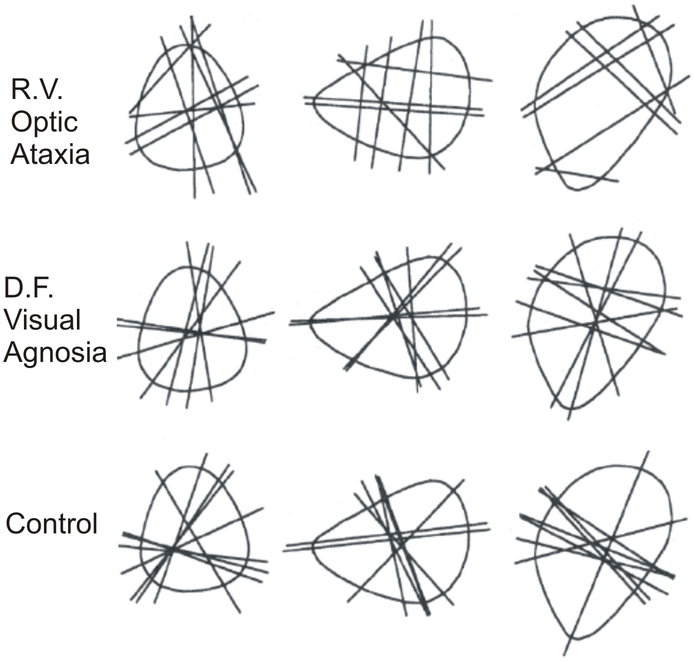


Figure 1.5: *The grasp lines (showing the chosen contact points) when grasping different objects for patient R.V. (optic ataxia), patient D.F. (visual form agnosia) and a control subject. Whereas D.F. and the control subject chose stable grasp points patient R.V. was not able to select appropriate contact positions. Adapted from Milner and Goodale (1995).*

Concerning the temporal aspect, it was reported by Milner et al. (2001) that the visuomotor performance of another ataxic patient (I.G.) was improved when the grasping movement had to be pantomimed after a delay. Showing exactly the complementary pattern of results than patient D.F. it was concluded that the movements executed after a delay were guided "off-line" by the stored object representation of the intact ventral stream. Furthermore, these findings are regarded as corroboration of the different timing behavior of the dorsal and the ventral stream as proposed by the perception–action model.

The double dissociation between perceiving the shape of an object and using this information to guide the fingers when grasping the object is interpreted as strong evidence for two separate neuronal systems acting relatively independently. However, this evidence has also been criticized. First of all, it has to be mentioned that the precise functional nature of the lesions of patient D.F. as well as R.V. still remains obscure. A very recent study of Schenk (2006) has shown that the deficits of D.F. do not necessarily support an interpretation in the terms of the Milner and Goodale (1995) model. Schenk (2006) demonstrated that D.F.'s performance was impaired in allocentric conditions and preserved in egocentric conditions for both perceptual and motor tasks. Thus, D.F.'s performance depended on how the object information was presented and not on which behavioral response was required. This finding challenges one of the main predictions of the perception–action model. Furthermore, it was argued by Rossetti, Pisella, and Vighetto (2003) that also the evidence coming from the studies of optic ataxia patients does not necessarily support the double–dissociation between action and perception. In this review they argue that optic ataxia seems to result from a specific impairment of immediate visuomotor control rather than of visually guided action as a whole.

Illusion studies Since most lesions are not necessarily restricted to one circumscribed brain area, and other areas can take part of the functioning of the damaged ones, arguments drawn from lesioned brains may not always be valid for understanding normal brain functions. Thus, if perception and action were really guided by different representations it would be more convincing to show this dichotomy in normal subjects.

A frequently used paradigm to show the perception–action dissociation in normal subjects is the study of visual illusions, e.g., the Ebbinghaus illusion (Figure 1.6). This illusory figure consists of two central circles of equal physical size which are presented side by side. One central circle is surrounded by smaller circles whereas the other is surrounded by larger circles leading to the situation that the perception of the relative size of the central circle does not correspond to its real size. Thus, people's perceptual judgments of the size of one element of the pattern are influenced by the other elements in the surround. It is claimed by the perception–action model that the ventral pathway, which is concerned with conscious perceptual processes, codes the size of an object relative to the context (allocentric frame of reference). In contrast, the dorsal pathway which represents the visuomotor system calculates the object's position with respect to the body and the size of the object in absolute and precise metrics (egocentric frame of reference). Thus, the representation acquired by the ventral pathway is expected to be deceived by the illusion whereas the dorsal pathway is expected to be insensitive to the illusion meaning that actions directed to the illusion cannot be deceived.

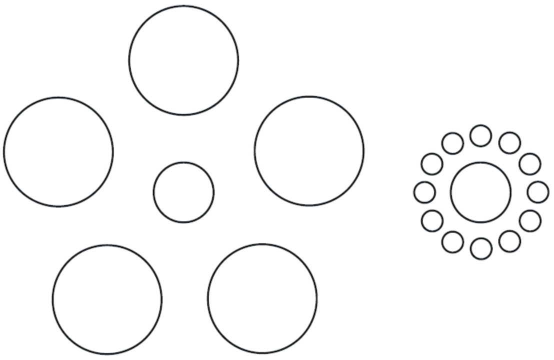


Figure 1.6: *The Ebbinghaus illusion. The central circles in the two arrays are the same size, but the one on the left, surrounded by larger circles, appears to be smaller than the one on the right, surrounded by smaller circles. Figure adapted from Franz et al. 2000.*

Numerous experiments have examined this question by comparing perceptual judgments of the size of the central target disc in the Ebbinghaus illusion with the size of the grip aperture when people reach out and pick up that disc (grip aperture reflects a good size estimate of the motor system, cf. section 1.2). Showing that the influence of the illusion was larger on perceptual judgments than on maximum grip aperture (MGA) some studies give evidence for the predictions of the perception–action model (e.g., Aglioti et al., 1995; Haffenden & Goodale, 1998, 2000b). However, in the last years a number of researchers have argued that the motor system is affected by an illusion to a similar degree as perception (e.g., Franz et al., 2000; Franz, 2001; Pavani et al., 1999; van Donkelaar, 1999; Dassonville & Bala, 2004). In short, it was argued that the apparent dissociation between perception and action reported by other studies using visual illusions is mainly due to methodological problems (Franz et al., 2000; Franz, 2003; Franz & Gegenfurtner, in press). Overall, literature on this topic remains to this day controversial (for review see Carey, 2001; Smeets & Brenner, 2006; Franz & Gegenfurtner, in press)

The above mentioned prediction of the perception–action model that dorsal and ventral stream are supposed to work on different time scales was also tested using illusion studies (mainly the Müller-Lyer illusion). It was argued that if a delay is introduced between the presentation of the illusion and the required movement initiation the dorsal representation decays. Thus, when a movement is initiated after a time delay, movement execution is thought to depend on the stored ventral representation which is deceived by the illusion. In that case, it is expected that the visual illusion affects the action. There are numerous studies showing exactly this increasing effect of the illusion in action tasks after a delay (e.g., Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Hu & Goodale, 2000; Westwood, Heath, & Roy, 2000; Westwood, McEachern, & Roy, 2001; Westwood & Goodale, 2003; Heath, Rival, Westwood, & Neely, 2005; for an alternative interpretation see, Franz, Hesse, & Kollath, 2007). Recently, an even stronger version of this proposed timing behavior of the dorsal and the ventral stream has been proposed: the "real–time view of action" (Westwood & Goodale, 2003; Westwood et al., 2003; Goodale et al., 2003, 2005).

According to this specification of the perception–action model it is useless to plan and store a motor program in advance. Instead, this very strong hypothesis suggests that the information required to execute an action is computed in real–time immediately before, and only when movement initiation is actually required. Consequently, the introduction of a delay between viewing an object and acting on it should lead to the decay of the dorsal representation which is thus no longer available for movement execution. In this case, the movement has to be carried out by the long–lasting representation of the ventral stream. According to the "real-time view" of action, the transition from the real-time visuomotor control system (dorsal) to the memory driven perceptual system (ventral) occurs as soon as the object is not visible at the moment movement initiation is required. If vision is suppressed at this moment dorsal real–time computations are unaccessible such that the motor system has to use the stored ventral representation. The importance of object visibility during the time interval needed for movement programming was tested directly in some studies using again pictorial illusions as stimuli. In these studies it was expected that the undeceived dorsal representation is used when vision is available during the movement or at least during the programming phase whereas introducing a delay prior to response initiation results in the use of the stored perceptual representation which is deceived by the illusion. Unfortunately, these studies also show ambiguous results since in some experiments grasping movements were also influenced by the illusion when the object was visible at movement programming (e.g., Westwood et al., 2001; Heath, Rival, & Binsted, 2004; Heath et al., 2005; for an alternative interpretation see, Franz et al., 2007). Considering the fact that it is still a matter of debate whether grasping movements resist visual illusions at all it remains therefore unclear whether different representations are used for visually guided and memory guided movements and if so, when exactly the representation is changed.

1.1.3 Conclusions

The two visual system hypothesis as proposed by Milner and Goodale (1995) has been very influential in proposing an alternative model of brain organization in which visual input is processed in two different pathways. However, the experimental evidence for the perception–action hypothesis is ambiguous. The validity of some of the empirical evidence originally presented in favor of the theory, has been put into question by recent experiments. In the light of these studies, a radical dichotomy between perception and action pathways, as initially proposed, seems no longer tenable. Moreover, in most of our every day actions, like picking up a cup of tea, the functions of the two streams cannot clearly be separated. For the control of such more complex, movements the involvement of both pathways would be expected suggesting that there are at least multiple interconnections between both systems. However, so far little has been said about how the two streams work together.

1.2 The grasping movement

1.2.1 Kinematics

Studies of grasping progressed with work of Napier (1956) classifying grasping movements into precision and power grip (Figure 1.7). Precision grip is characterized by the opposition of the thumb to one finger (mostly the index finger) whereas in the power grip all fingers are flexed to form a clamp against the palm. Which grasp type is chosen is largely determined by object related visual input. Most studies in grasping literature (in humans) are restricted to the examination of the precision grip.

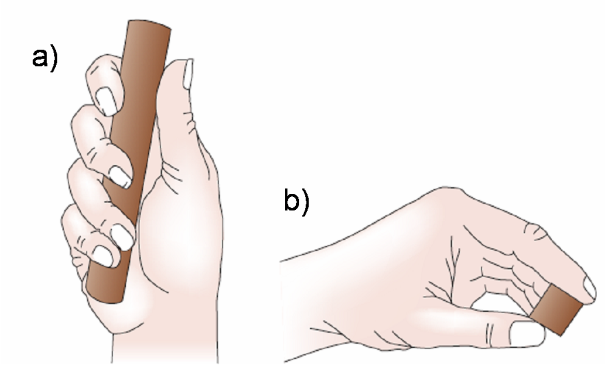


Figure 1.7: *Examples of the different grasp types defined by Napier (1956): a) power grip and b) precision grip. Reprinted from Castiello (2005).*

When executing a precision grip the pre–shaping of the hand is a highly stable motor pattern. This pattern corresponding to the separation between the index finger and the thumb was first described by Jeannerod (1981, 1984). He showed that during reach–to–grasp movements the fingers open gradually until they reach a maximum (larger than the actual size of the object), followed by a gradual closure of the grip until it matches the object's size (Figure 1.8). Maximum grip aperture (MGA) has thereby turned out to be a very useful measure to describe such movements. In short, MGA occurs in the second half of the movement (after about 60–75% of movement time), is linearly related to object size, and occurs later in movement time for larger objects (e.g., Jeannerod, 1981, 1984; Bootsma, Marteniuk, MacKenzie, & Zaal, 1994; Marteniuk, Leavitt, MacKenzie, & Athenes, 1990; Smeets & Brenner, 1999). In a metaanalysis on grasping studies Smeets and Brenner (1999) showed that the slope of the function relating MGA to object size takes in most cases a value between 0.7 and 0.8. Thus, MGA can be regarded as an early size estimate of the motor system. Moreover, MGA continues to be scaled to object size when visual feedback is reduced (Jeannerod, 1984) despite an overall increase in size suggesting that in this case a larger safety margin is preprogrammed to compensate for an increased spatial uncertainty (Wing, Turton, & Fraser, 1986; Jakobson & Goodale, 1991).

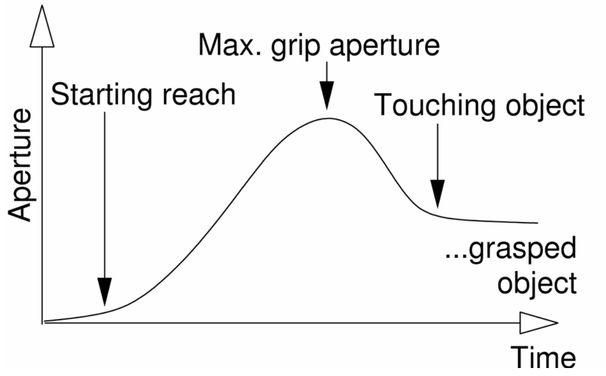


Figure 1.8: *Representation of a typical aperture profile (distance between index finger and thumb) when grasping an object. Maximum grip aperture occurs within 70% of movement completion. Adapted from Franz et al. (2005).*

1.2.2 Neuronal mechanisms

By using single cell recordings three main areas relating to grasping movements have been identified in the monkey cortex (Figure 1.9): the primary motor cortex (F1),the premotor cortex (PML/F5), and the anterior intraparietal sulcus (AIP) (for review see, Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Castiello, 2005).

Primary Motor Cortex (F1): The execution of accurate grasping movements requires the intactness of the primary motor cortex as well as the pyramidal tract.

Lesions in these structures (in monkeys) have been shown to result in a profound deficit in the control of finger movements and thus the ability to grasp normally (e.g., Lawrence & Hopkins, 1976; Lawrence & Kuypers, 1968b, 1968a). However, there are only few visually responsive neurons in F1 suggesting that the visuomotor transformations which are required for grasping occur in motor areas which are more closely connected to the visual system.

Premotor area F5: To grasp an object successfully the intrinsic properties of the object have to be transformed into motor actions. In monkeys two cortical areas being involved into these transformations have been identified: area F5 and the AIP. Single cell recordings during object–oriented motor actions have shown that most areas of area F5 are involved in grasping as well as other object related actions such as holding, tearing and manipulating (Rizzolatti et al., 1988). Furthermore, the neurons recorded in F5 code for grasping actions that relate to the type of the object to be grasped (e.g., precision grip) (e.g., Murata, Gallese, Luppino, Kaseda, & Sakata, 2000). Visual responses, meaning that neurons fire when visual stimuli are presented without any movement requirements, were observed in 20-30% of the F5 neurons. Moreover, a relationship between the type of prehension that is coded by the cell and the size of the stimulus that is effective in triggering the neuron was reported. For example, precision–grip neurons were only activated by the presentation of small visual objects. Furthermore, another type of neurons responded when the monkey sees movements, similar to those coded by the neuron, but which are executed by the experimenter or another monkey (termed "mirror neurons" by DiPellegrino, Klatzky, & McCloskey, 1992; see also Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). In short, area F5 seems mainly to be responsible in selecting the most appropriate motor prototype for a specific action.

AIP: While most neurons in F5 are concerned with a particular segment of the action - some neurons mainly fire at the beginning of the grasping movement (finger extension) and others during the last part of the movement (finger flexion) - AIP neurons seem to represent the entire action. Moreover, most AIP neurons show visual responses to three–dimensional objects suggesting that AIP is mainly involved in providing 3D descriptions of objects for the purpose of manipulation (Murata et al., 2000).

Binkofski et al. (1998) have shown that the human homologue of area AIP (besides other areas) plays also an important role in grasping in humans (cf. Figure 1.9). In line with the results obtained for monkeys, grasping in human patients with lesions in the anterior portion of the intraparietal sulcus (aIPS) was impaired while the reaching movement remained relatively intact. Recent studies suggest that aIPS is also critically involved in the on–line control of actions (for review see, Tunik, Rice, Hamilton, & Grafton, 2007). Combining a perturbation paradigm with the transcranial magnetic stimulation (TMS) method Tunik, Frey, and Grafton (2005) could show that the corrective computations assuring that the current grasp plan matches the current context and sensorimotor state are performed within aIPS.

Patients with lesions of the superior parietal lobule (SPL) showed also diverse deficits in the control of grasping movements (cf. optic ataxia). For example, patient V.K. showed a relatively normal early phase of the grip formation but on–line control in the end of the movement was strongly impaired resulting in numerous secondary peaks of the aperture profile (Jakobson et al., 1991). Another patient A.T. suffering from a damage of the SPL and secondary visual areas as well as some damage of the inferior parietal lobule (IPL) could not open the hand appropriately in anticipation of the grasp (preshaping deficit) and did not adjust the grasp to object size (Jeannerod et al., 1994).

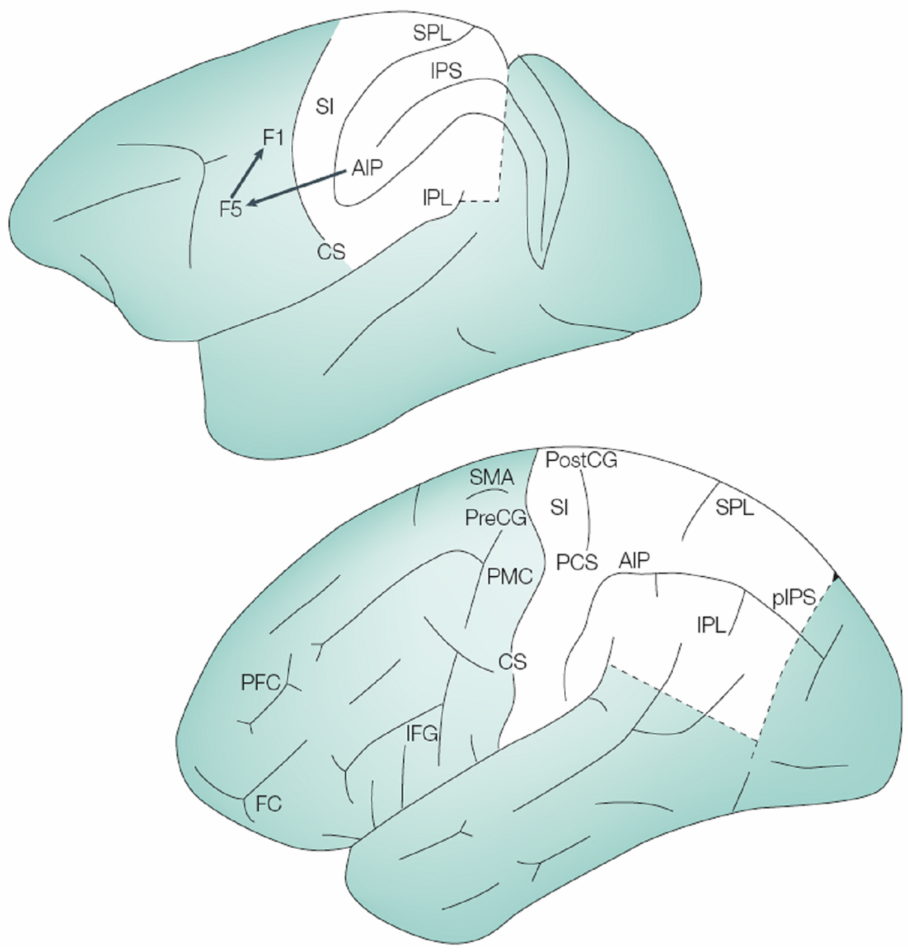


Figure 1.9: *Comparison between neural circuits for grasping in macaque monkeys and humans (lateral view). For the monkey, the visuomotor stream for grasping (AIP–F5) and the stream from F5 to F1 are indicated by the arrows. Grasping areas in humans (identified by neuroimaging studies). AIP, anterior intraparietal area; CS, central sulcus; FC, frontal cortex; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; IPS, intraparietal sulcus; PCS, postcentral sulcus; PFC, prefrontal cortex; pIPS, posterior intraparietal sulcus; PMC, premotor cortex; PostCG, postcentral gyrus; PreCG, precentral gyrus; SI, primary somatosensory cortex; SMA, supplementary motor area; SPL, superior parietal lobule. Cortical areas that control grasping are also connected with basal ganglia and cerebellar circuits which are also involved in grasping but are not shown in the figure. Reprinted from Castiello (2005).*

1.2.3 Models

The kinematics of grasping movements are influenced by different task demands, such as the amount of feedback available during the movement, changes in object size or object shape (but also others which are not discussed here e.g., fragility (Savelsbergh, Steenbergen, & vanderKamp, 1996), texture (Weir, MacKenzie, Marteniuk, & Cargoe, 1991) and weight (Weir, MacKenzie, Marteniuk, Cargoe, & Fraser, 1991; Johansson & Westling, 1988; Gordon, Forssberg, Johansson, & Westling, 1991). Although, some movement parameters are affected by these modifications the resulting grip pattern remains surprisingly stereotypical and seems to be very adaptive to different conditions and perturbations. Thus, there have been many attempts to describe grasping movements formally.

One of the first formalizations was done by Jeannerod (1984) describing grasping as a movement consisting of two components: the transport component which carries the hand to the location of the object (proximal component) and the grasp component which shapes the hand in anticipation of the grip (distal component). Since MGA is relatively constantly reached at about two thirds of the movement duration, Jeannerod (1984) stated that the two components work independently but are temporally coupled. This classical description of grasping is still very influential and most models have concentrated on the precise nature of this coupling by proposing several timing mechanisms (e.g., Marteniuk et al., 1990; Bootsma & van Wieringen, 1992; Hoff & Arbib, 1993; Hu, Osu, Okada, Goodale, & Kawato, 2005). Recently, Mon-Williams and Tresilian (2001) proposed a "simple rule of thumb" which predicts the timing of MGA by assuming that the ratio of the duration of the opening and closing phase of the fingers is proportional to the ratio of the amplitudes of the two phases. Even though the simplicity of this description seems convincing it does not hold for many empirical results (e.g., the time of MGA is predicted much earlier by the model than is typically observed in empirical studies). Besides these simple primarily descriptive models there are more complex ones modeling not only certain movement parameters but the whole trajectory of the fingers.

For example, Rosenbaum and colleagues (Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; Meulenbroek, Rosenbaum, Jansen, Vaughan, & Vogt, 2001) simulated grasping movements using the theory of posture-based motion planning. It is assumed that grasping movements are planned on the basis of a task specific constraint hierarchy to perform optimally under certain conditions. From a set of possible stored goal postures the best one for the task is chosen and then converted into a smooth straight line movement in joint space. This complex model mainly focuses on the behavior of the different joints during grasping. In contrast, the more prominent model of Smeets and Brenner (1999) uses the minimum jerk approach to formalize grasping movements. The key assumption of their model is that grasping is nothing else than moving the fingers to predetermined object positions suitable for grasping. The fingers approach these positions orthogonally. The advantage of this model is that it does not discriminate between the grasp and the transport component and therefore does not have to deal with their coupling. Moreover, the model can efficiently simulate the different aspects of grasping movements and predicts correctly how changes of object properties such as size, shape, fragility, or changed task requirements such as limited perception and time constraints affect grasping kinematics.

1.2.4 Conclusions

In summary, a lot of research has been done in the last fifty years to investigate the grasping movements in monkeys and humans. Although good progress was made in investigating the kinematics of the grasping movement and the influence of different task requirements, our knowledge about the underlying neuronal mechanisms transforming the visual input into the appropriate motor output is far from conclusive. Examining the relationship of visual input and motor output on a behavioral level might thus be a first step to understand the coupling of visual and motor processes in more detail.

1.3 Outline of the thesis

In this thesis the use of visual information in grasping is investigated in humans using behavioral approaches. The thesis consists of three studies:

In the first study (chapter 2) the effects of visual memory on grasping kinematics are investigated by introducing different delays between object presentation and movement initiation. In particular, we tested for the predictions of the "real–time view" of motor programming stating that a transition of the representation used (from dorsal to ventral) occurs after a delay. Contrary to the real-time view of motor programming we found no indication for a transition from one to another representation guiding the movement. Results rather suggest that the observed changes in grasping kinematics after a delay are due to an exponential decay of the visuomotor information over time and are thus comparable to what is known from memory research.

The second study tests for another prediction of the real–time view of motor programming stating that the metric aspects of a visually guided movement are always calculated de novo and in real-time suggesting that movements to visible targets are not influenced by prior visual experience. Results showed that the kinematics of visually guided grasping can also be influenced by prior visual experience challenging again the notion of the real–time view. Therefore, this study provides further evidence that perception and memory are involved in the execution of visually guided movements.

In the third study we examined the corrective processes during grasping movements. We were especially interested in how adjustments of the grip are accomplished during movement execution and whether vision of the hand is used to control the grip on-line. To this end, we applied a size perturbation paradigm meaning that objects changed their size during the movement. Results indicate that vision of the hand is not necessary to adjust the grip indicating that the planned motor program is smoothly adjusted using feed–forward mechanisms.

Reading advice

Every chapter of this thesis is written as a separate scientific study intended for publication in scientific journals. Thus, each chapter has its own Introduction and Conclusion section making it possible to read each chapter independently from the others. The disadvantage of this writing style is that those who aim at reading the whole work might find repeating information.

Chapter 2

Memory mechanisms in grasping

Abstract

The availability of visual information influences the execution of goal–directed movements. This is very prominent in memory conditions, where a delay is introduced between stimulus presentation and execution of the movement. The corresponding effects could be due to a decay of the visual information or to different processing mechanisms used for movements directed at visible (dorsal stream) and remembered (ventral stream) objects as proposed by the two visual systems hypothesis. In three experiments, the authors investigated grasping under full vision and three different delay conditions with increasing memory demands. Results indicate that the visuomotor information used for grasping decays exponentially. No evidence was found for qualitative changes in movement kinematics and the use of different representations for visually guided and memory guided movements. Findings rather suggest that grasping after a delay is similar to grasping directed to larger objects under full vision. Therefore, the authors propose that grasping after a delay is guided by classic memory mechanisms and that this is reflected in an exponential effect on maximum grip aperture in grasping.

2.1 Introduction

Visual information plays an important role for the planning and execution of goal-directed movements such as grasping. There are two ways in which visual information can be used to optimize a grasping movement towards an object. First, when planning the movement visual information is necessary to specify the properties of the object such as its shape, size, and orientation. These physical characteristics must be visually processed and then transformed into motor signals to obtain the appropriate hand shape for grasping (Jeannerod, 1981). Second, during movement execution visual information can be used to monitor the movement on-line (e.g., Woodworth, 1899), meaning that the grip can be adjusted and corrected if necessary. Although, it is plausible that visual feedback improves the precision of a goal-directed movement, it is still a matter of debate in which way visual information is exactly used during the execution of grasping movements (e.g., Jeannerod, 1984; Connolly & Goodale, 1999; Schettino, Adamovich, & Poizner, 2003; Winges, Weber, & Santello, 2003). In this study, we investigated the use of visual information by varying the amount of visual information available and thereby increasing the memory load successively (cf. Figure 2.1).

Specifically, we focused on three questions: How is the movement affected by preventing visual feedback during movement execution (cf. CL vs. OL-Move conditions in Figure 2.1)? Is there any evidence that object visibility during the programming phase of the movement is crucial for movement execution (OL-Move vs. OL-Signal conditions)? What happens to the movement kinematics if longer delays between object presentation and movement execution are introduced (OL-Signal vs. OL-Delay condition)? We will show that there are systematic influences that can be described by an exponential decay of the visual information similar to the findings in memory research (e.g., Ebbinghaus, 1885; Wickelgren, 1970; Loftus, Duncan, & Gehrig, 1992; R. B. Anderson & Tweney, 1997). This leads to the interesting situation that we can use grasping to tap into memory mechanisms. This opens an avenue for using relatively complex actions (as grasping and pointing) to investigate cognitive processes (as memory) thereby following a recent suggestion of Nakayama, Song, Finkbeiner, and Caramazza (2007). But, at first we want to summarize what is known so far about the use of visual information during grasping movements.

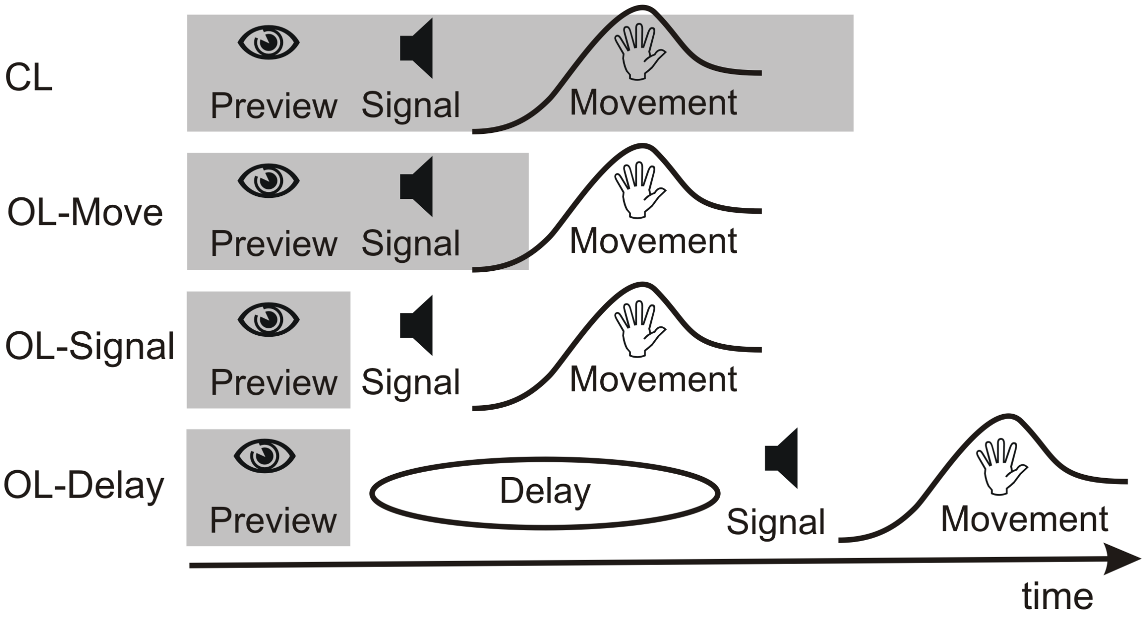


Figure 2.1: *Event sequences for Closed-loop (CL), Open-loop until movement initiation (OL-Move), OL until start signal (OL-Signal) and OL-5 s delay (OL-Delay) condition. The gray shaded bar indicates the time-interval during which object and hand are visible. These conditions were used in Experiment 1 and Experiment 2. Further details are given in the text.*

Many studies have investigated the use of visual feedback during grasping by either preventing vision of the moving hand alone or by preventing vision of object and hand simultaneously during the movement (often referred to as open-loop; e.g., Jeannerod, 1984; Jakobson & Goodale, 1991; Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Schettino et al., 2003). Most of these studies agree that movement time (MT) tends to increase when visual feedback is reduced and that this increase is mostly due to a longer deceleration phase of the movement caused by a slower approach to the object (Wing et al., 1986; Berthier et al., 1996; Schettino et al., 2003). Moreover, several studies reported a larger maximum grip aperture (MGA) between index finger and thumb which occurred earlier in MT when visual feedback was removed (e.g., Wing et al., 1986; Jakobson & Goodale, 1991; Berthier et al., 1996). Since MGA continues to be scaled for object size in the reduced feedback conditions it was proposed that a larger safety margin is preprogrammed compensating for spatial uncertainty (Wing et al., 1986; Jakobson & Goodale, 1991). In short, visual feedback of the hand during grasping seems especially important in the latter stages of the movement when the fingers close around the object. The overall pattern of the movement, however, such as the scaling of the aperture to object size and the gradual posturing of the fingers to object shape seems to remain unaffected by occluding vision (e.g., Connolly & Goodale, 1999; Santello, Flanders, & Soechting, 2002; Winges et al., 2003).

When grasping an object without visual feedback some internal representation of the object has to be acquired during the planning phase of the movement. This internal representation which contains the intrinsic characteristics of the object and its position in space can then be used to guide actions when visual information about the environment is unavailable. Goodale and Milner (1992) argue that the representation used for performing an action toward an object is fundamentally different from the representation acquired by just perceiving this object. The basis of this assumption is the attribution of the anatomically well discriminable ventral and dorsal stream to a perception versus action pathway. According to this view, known as the ”two visual systems” hypothesis, the ventral stream is mainly involved in object identification and recognition whereas the dorsal stream mainly processes visual information for the control of actions, such as grasping (see also: Milner & Goodale, 1995). Moreover, both streams are assumed to process information on different time scales (Goodale, Jakobson, & Keillor, 1994; Milner et al., 2001; Rossetti, 1998). In order to identify and later recognize objects, viewpoint independent information must be stored over a long time in the ventral stream. In contrast, for grasping an object successfully its spatial position relative to the body needs to be taken into account. Given that the relative positions of observer and target object can change quickly, the egocentric coordinates of the object's position only need to be available for a few milliseconds. Because it therefore seems useless to store the motor program, it was proposed that the information required for actions are computed in real-time immediately before movement initiation (Westwood & Goodale, 2003; Westwood et al., 2003).

Consequently, the introduction of a delay between viewing an object and acting on it should lead to the decay of the dorsal representation which is thus no longer available for movement execution. It is argued that in this case the movement is carried out by the long-lasting representation of the ventral stream. According to this "real-time view" of action, which can be regarded as a specification of the "two visual systems" hypothesis, the transition from the real-time visuomotor control system (dorsal) to the memory driven perceptual system (ventral) occurs as soon as the object is not visible at the moment when movement initiation is actually required (Goodale et al., 2003, 2005). That is, the time period between start signal and movement initiation is assumed to be critical for movement programming. If vision is suppressed during this "RT-interval" dorsal real-time computations are unfeasible such that the motor system has to use the stored ventral representation. Strictly speaking, object visibility during the RT-interval determines whether dorsal or ventral information is used to guide the action (Westwood & Goodale, 2003; Westwood et al., 2003; Goodale et al., 2003, 2005).

One of the first studies examining the different temporal properties of the two streams comes from Goodale, Jakobson, and Keillor (1994) demonstrating that pantomimed grasping movements executed after a delay of 2 s after viewing the object show different kinematic properties than movements executed in real-time. This result was considered as evidence that pantomimed reaches were driven by the stored ventral information about the object resulting in a changed grasping behavior. However, it remained unclear whether the observed kinematic differences were indeed due to the temporal delay or due to the fact that in the delay conditions the object was not grasped and therefore no haptic feedback was presented (Westwood, Chapman, & Roy, 2000; Hu, Eagleson, & Goodale, 1999).

In a study of Hu et al. (1999), avoiding the limitations of the pantomimed grasping paradigm, participants had to grasp objects in different visual memory conditions: closed-loop (full vision of object and hand during the movement), open-loop (participants initiated their grasp as soon as the object was presented and it remained visible for 300 ms) and an open-loop delay condition (object was visible for 300 ms but the grasp was initiated 5 s after object presentation). In both open-loop conditions vision of the object and the hand was prevented. Hu et al. (1999) found no differences in any kinematic measures between the closed-loop and the open-loop condition in which the object was visible during movement initiation. They concluded that in both conditions the action was driven by the real-time visuomotor transformations of the dorsal stream. In contrast, movements executed in the open-loop-delay condition (after 5 s) required more time, showed a larger MGA, and altered velocity profiles suggesting that the stored perceptual information of the ventral stream was used.

However, one might want to argue that these results do not necessarily support an interpretation in terms of the Milner and Goodale (1995) theory. Indeed, the observed kinematic differences caused by a delay might simply reflect a decay of information in the visuomotor system over time and not the use of qualitatively different visual representations. Moreover, the effects of introducing a delay on grasping kinematics are similar to those reported for the reduction of visual feedback during the movement by preventing vision of the moving hand (larger MGA which occurs earlier in time and prolonged MT). Therefore, the study of Hu et al. (1999) contradicts earlier observations that preventing vision of the hand and the target object results in changed movement kinematics because they did not find a difference between their closed-loop and open-loop condition.

As mentioned above, according to the real-time view of action, object visibility during the period between the start signal and movement initiation should be crucial for the kind of representation used. Therefore, the kinematics of grasping movements executed under full vision should not differ from those in which the object remains visible until movement initiation. On the other hand, introducing only a very short delay should result in altered kinematics which are relatively independent of the length of delay since the stored ventral information is used in these cases. Up to now, the importance of object visibility during the RT-interval that should cause the shift from direct visuomotor control to perception-based action control was tested directly only in studies using pictorial illusions as stimuli (e.g., the Ebbinghaus Illusion or the Müller-Lyer Illusion). In these studies it was expected that when vision is available during the movement or at least during the programming phase the undeceived dorsal representation is used whereas introducing a delay prior to response initiation results in the use of the stored perceptual representation which is deceived by the illusion (e.g., Hu & Goodale, 2000; Westwood, Heath, & Roy, 2000; Westwood et al., 2001; Westwood & Goodale, 2003; Heath et al., 2005). Unfortunately, these studies also show ambiguous results since in some experiments grasping movements were also influenced by the illusion when the object was visible during the RT-interval. (e.g., Westwood et al., 2001; Heath et al., 2004, 2005). Considering the fact that it is still a matter of debate whether grasping movements resist visual illusions at all (Franz et al., 2000; Franz, 2001; Pavani et al., 1999; Dassonville & Bala, 2004) it remains still unclear whether different representations are used for visually guided and memory guided movements and if so, when exactly the representation is changed.

In the present study we wanted to clarify the effects of visual memory on grasping kinematics using different delays and two kinds of very basic stimuli (bars and discs). We were especially interested in the differential effects of object visibility during movement execution, and object visibility during the RT-interval. Therefore, we designed four different delay conditions (similar to those of Westwood et al., 2001) increasing memory demands successively: closed loop (CL), open-loop with full vision until movement initiation (OL-Move), open-loop with full vision until start-signal (OL-Signal) and a open-loop 5s-delay (OL-Delay) condition (cf. Fig. 2.1). If the real-time view of motor programming is correct then the biggest difference in movement kinematics should occur between the OL-Move and the OL-Signal condition because the difference between these conditions is that object visibility is suppressed during the RT-interval in the OL-Signal condition. This should change the internal representation from dorsal (OL-Move) to ventral (OL-Signal). If, however, the visuomotor information simply decays over time one would expect differences between all conditions investigated (cf. Fig. 2.2). We used two different kinds of goal objects and a wide range of object sizes (1-10 cm) to obtain as general results as possible and because it has been demonstrated that changing object shape might have considerable effects on the kinematics of an executed movement (Zaal & Bootsma, 1993). Since studies examining the influence of reduced visual feedback and longer delays so far have yielded inconsistent results we also decided to use larger sample sizes than usual to avoid problems with statistical power and to obtain reliable estimates of the effect sizes (Maxwell, 2004).

2.2 Experiment 1

In this experiment we investigated the effects of different delays (higher memory load) on grasping kinematics using simple stimuli (bars of different lengths). We were especially interested in the effects of suppressing visual feedback during movement execution and the additional effects of preventing object visibility during the RT-interval. According to the real-time view of motor programming a transition from the use of the real-time dorsal to the stored ventral representation should take place during this interval. Therefore, movement kinematics in conditions in which vision of the object is available during movement initiation (CL and OL-Move cf. Fig. 2.1) should differ qualitative from movements initiated without object visibility (OL-Signal and OL-Delay).

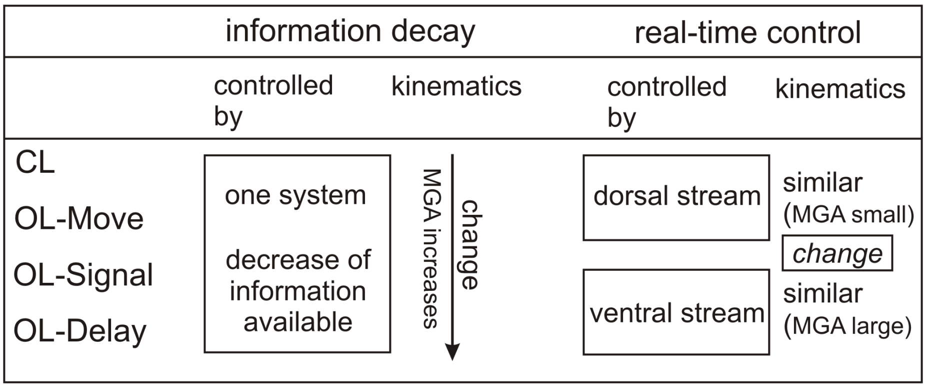


Figure 2.2: *Predictions of the real-time hypothesis compared to the assumption that visuomotor information decays over time. According to the real-time hypothesis the transition from the use of the dorsal stream representation to the use of the ventral stream representation occurs if the object is not visible when the movement is initiated. Movements executed by the dorsal stream are expected to differ qualitatively from movements executed by the ventral stream. The hypothesis of information decay predicts that only one representation is used which decays over time. Thus, it is expected that movement kinematics change continuously with longer delays.*

2.2.1 Methods

Participants Forty-eight undergraduate and graduate students of the University of Giessen (21 males, 27 females, mean age = 24, SD = 4) participated in the experiment. They were paid 8 Euro per hour for participation. One experimental session lasted about 80 minutes. All participants were right-handed by self report and had normal or corrected-to-normal visual acuity.

Apparatus and Stimuli Participants sat on an adjustable chair using a chin rest to maintain a constant head position throughout the experiment. They looked at a white board (24 x 45 cm) which served as presentation surface for the stimuli. The board was slightly tilted and therefore perpendicular to gaze direction. The viewing distance to the center of the board was 50 cm. Three black plastic bars of different lengths (39 mm, 41 mm, and 43 mm) but constant width (8 mm) and depth (5 mm) served as stimuli. They were presented in the centre of the board. The trajectories of the finger movements were recorded by an Optotrak 3020 system (Northern Digital Incorporation, Waterloo, Ontario, Canada) at a sampling rate of 200 Hz. Light weight, small metal plates with three infrared light-emitting diodes (IREDs) were attached to the nails of thumb and index finger of the right hand (using adhesive pastels: UHU-patafix, UHU GmbH, Bühl, Germany). Prior to the experiment a calibration procedure was used to measure the typical grasp points of the fingers relative to the three markers on the plate. Using mathematical rigid–body calculations, this allowed for an accurate calculation of the grasp points of index finger and thumb. In order to detect the exact moment when the target object was touched, an additional IRED was embedded in the board. Each target had a little mirror on the left side reflecting the signal of the embedded IRED, which was registered by the Optotrak (cf. Franz, Scharnowski, & Gegenfurtner, 2005, Fig. 3f, p. 1363). As soon as the target bar was moved the Optotrak received a velocity signal indicating the exact time of contact with the stimulus. To control object visibility participants wore liquid-crystal shutter goggles (PLATO Translucent Technologies, Toronto, Ontario; Milgram, 1987).

Procedure Participants started each trial with the index finger and thumb of the dominant right hand located at the starting position. The distance between starting position and object was 40 cm. The shutter goggles were opaque between all trials while the experimenter placed the object on the board. At the beginning of each trial the goggles switched to the transparent state for a preview period of 1 s. Participants were instructed to view the object during this preview period but had to wait with their grasp until an auditory signal was given. In response to this auditory signal, participants grasped the bar along its major axis, lifted it, placed it in front of them on the table, and moved their hand back to the starting position. Subsequently, the experimenter returned the bar and prepared the next trial. There were four different experimental conditions which differed in the amount of visual information and memory demands (see Fig. 2.1).

In the "closed-loop" (CL) condition the auditory signal directly followed the preview period and the shutter goggles remained open for another 4 s, such that participants could see both the object and their hand during grasping. In the "open-loop until movement initiation" (OL-Move) condition the auditory signal was also given directly after the preview period, but the goggles turned opaque when the finger left the starting point (i.e., after both fingers had moved more than 20 mm away from the starting position). This means that the occlusion of vision during grasping was triggered by the movement of the fingers and that participants executed their grasp without seeing object and hand. In the "OL until start signal" (OL-Signal) condition the auditory signal and the changing of the shutter goggles to the opaque state occurred simultaneously after the 1 s preview phase, independent of finger movements. Similar to the previous condition neither object nor hand were visible during grasping, but this time the visual occlusion was triggered by the auditory signal and therefore occurred slightly earlier than in the OL-Move condition. The main difference between the OL-Move and the OL-Signal condition was therefore whether the target object was visible during the RT-interval or not. Finally, there was a "OL-5s delay" (OL-Delay) condition in which a 5 s delay was inserted between the preview period and the auditory start signal. During this 5 s delay and the following grasping movement the goggles remained opaque such that the participants had to remember the object for more than 5 s. This condition therefore posed the highest memory demands.

In all conditions participants were allowed 4 s to execute the movement (from the start signal until having removed the bar by at least 50 mm from the board). If this time limit was exceeded, the trial was classified as an error and was repeated later in the experiment at a random position. The different visual conditions were presented in blocks of 30 trials (10 trials per stimulus-length) with six practice trials preceding each condition. The order of blocks was counterbalanced across participants and the presentation sequence within each condition was in pseudo random order.

Data Analysis The finger trajectories were filtered off-line using a second-order Butterworth Filter employing a low-pass cut-off frequency of 15 Hz. Movement onset was defined by a velocity criterion. The first frame in which the index finger or the thumb exceeded a velocity threshold of 0.025 m/s was taken as movement onset. Reaction time (RT) was defined as the time between the auditory start signal and movement onset. The touch of the object was also defined by a velocity signal given by the mirror attached to the objects. The first frame in which this signal exceeded a velocity threshold of 0.01 m/s was taken as the touch of the object. MT was defined as the time between movement onset and touch of the object. Furthermore, different parameters of the aperture profile (difference between index finger and thumb) were analyzed: MGA was defined as the maximum distance between thumb and index finger during MT. Time to MGA was analyzed as absolute time (time from movement onset until MGA) and relative time (time of MGA as percentage of MT).

To characterize the transport component of the movement we calculated the midpoint between index finger and thumb. From these data we determined peak velocity and relative time to peak velocity of the hand. We used this as a measure of wrist velocity and thereby as indication of the transport component of the movement.

Data were analyzed using repeated measures analysis of variance (ANOVA) and the Greenhouse-Geisser correction (Greenhouse & Geisser, 1959). If not stated otherwise we performed repeated measures ANOVA using the Greenhouse–Geisser correction if a factor had more than two levels. This corrects for possible violations of the sphericity assumption in repeated measure data. For the Greenhouse–Geisser correction the parameter ϵ is estimated ($0 < \epsilon_{min} \leq \epsilon \leq 1$) which is used to adjust the degrees of freedom of the F–distribution. If $\epsilon = 1$ no violation of sphericity was detected and the Greenhouse–Geisser correction has no effect. If $\epsilon < 1$ the resulting test is more conservative than if no correction was performed (Greenhouse & Geisser, 1959; Vasey & Thayer, 1987; Jennings, 1987). Values are presented as means ± standard errors of the mean (between subjects). Post-hoc contrasts were carried out using Fisher's LSD (least significant difference) testing procedure. A significance level of $\alpha = 0.05$ was used for all statistical analyses.

2.2.2 Results

We examined the changes of kinematic parameters due to the different vision conditions. The main variable we were interested in was MGA (maximal distance between index finger and thumb). Therefore, a 4 (vision condition) x 3 (object size) repeated measures ANOVA was applied to the data. As expected, MGA was significantly affected by the vision condition, $F(3, 141) = 168.64, \epsilon = 0.68, p < 0.001$, and by object size, $F(2, 94) = 68.80, \epsilon = 0.83, p < 0.001$ (cf. Fig. 2.3a). There was no significant interaction ($p = 0.64$). More interesting are the differences between the four vision conditions. All vision conditions differed significantly from each other ($p < 0.001$ for all pairwise comparisons). The largest increase in MGA was observed between the CL and the OL-Move condition. Participants opened their hand in the OL-Move condition $15.4mm \pm 1.0mm$ wider than in the CL condition. This result is in accordance with most of the studies examining the effect of suppressing visual feedback during movement execution (e.g., Wing et al., 1986; Jakobson & Goodale, 1991; Berthier et al., 1996). However, it is in contrast to the findings of Hu et al. (1999) and to the assumption that movements in which vision is available during the programming phase do not differ from movements executed under full vision. Removing vision a little earlier, at the time of the start signal, had only a small additional effect on MGA (difference of OL-Move and OL-Signal condition: $3.5mm \pm 0.8mm$). The introduction of a 5 s delay also causes only a small extra increase in MGA (difference of OL-Signal and OL-Delay: $4.0mm \pm 0.9mm$).

Furthermore, we analyzed the absolute timing of MGA (time between RT and MGA): time until MGA was influenced significantly by the vision condition, $F(3, 141) = 34.15, \epsilon = 0.90, p < 0.001$, but not by object size, $F(2, 94) = 0.46, \epsilon = 0.95, p = 0.64$ (cf. Fig. 2.3b). Pairwise comparisons revealed that the OL-Move condition ($674ms \pm 21ms$) and the OL-Signal condition ($673ms \pm 17ms$) did not differ ($p = 0.93$) whereas all other differences were highly significant (all $p < 0.001$). Therefore, object visibility during the RT-interval had no effect on the timing of MGA. However, again there was a considerable difference between the CL and the OL-Move condition ($58ms \pm 15ms$), indicating that object visibility during movement execution has stronger effects than object visibility during movement programming. There was no significant interaction ($p = 0.46$).

A similar pattern of results was obtained when analyzing MT for the different conditions. MT was significantly affected by the vision conditions, $F(3, 141) = 106.66, \epsilon = 0.88, p < 0.001$, but not by object size, $F(2, 94) = 1.61, \epsilon = 0.99, p = 0.21$ (cf. Fig. 2.3c). All pairwise comparisons were significant ($p < 0.01$). The difference between CL and OL-Move was again larger than the difference between OL-Move and OL-Signal ($150ms \pm 21ms$ vs. $58ms \pm 20ms$). Also movements in the OL-Delay condition took on average $221ms \pm 27ms$ longer than movements in the OL-Signal condition. There was no significant interaction between vision condition and object size ($p = 0.39$).

Finally, we calculated the relative time to MGA which confirmed the differences between vision conditions, $F(3, 141) = 36.37, \epsilon = 0.65, p < 0.001$ (cf. Fig. 2.3d). As before, all pairwise comparisons between the four vision conditions were significant ($p < 0.001$). There was no main effect of object size, $F(2, 94) = 2.33, \epsilon = 0.99, p = 0.10$ and no significant interaction ($p = 0.86$).

Furthermore, we were interested in the scaling function of MGA to object size in the different delay conditions. It might be possible that after a delay the grip is more sensitive to physical changes of object size resulting in a steeper slope of the scaling function. Grip aperture was scaled to object size in all four vision conditions (cf. Figure 2.3a). The slopes were highest in the CL condition (0.7 ± 0.07 at MGA), smaller but almost equal in the OL-Move and OL-Signal condition (0.58 ± 0.09 and 0.56 ± 0.1 at MGA), and still somewhat smaller in the OL-Delay condition (0.46 ± 0.13 at MGA). However, the repeated-measures ANOVA revealed no main effect of vision condition on the slopes, $F(3, 141) = 1.10, \epsilon = 0.94, p = 0.35$. Thus, there was no

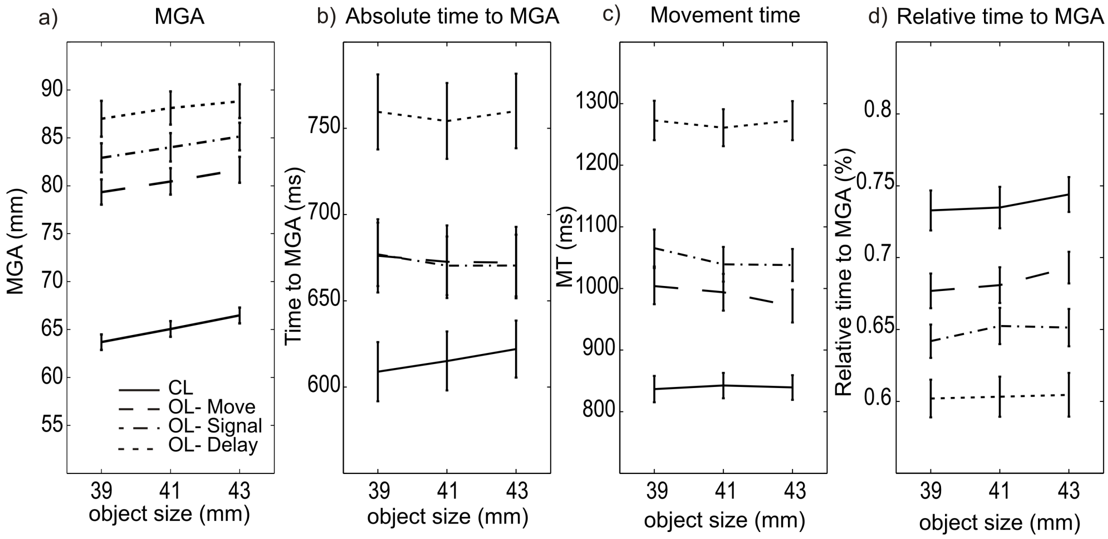


Figure 2.3: *Experiment 1: The effects of delay on: (a) MGA, (b) absolute time to MGA, (c) MT, and (d) relative time to MGA when grasping bars of three different lengths (39, 41 and 43 mm). All error bars depict ± 1 SEM (between subjects)*

increase (or decrease) in the sensitivity of grip scaling to physical changes of object size with increasing delay.

To characterize the transport component of the movement peak wrist velocity and the relative time to peak wrist velocity were calculated. Peak wrist velocity decreased with increasing delay. The 4 (vision condition) x 3 (object size) repeated measures ANOVA confirmed a significant main effect of vision condition, $F(3, 141) = 27.80, \epsilon = 0.95, p < 0.001$. Post-hoc tests revealed no significant difference between OL-Move and OL-Signal condition $(0.004m/s \pm 0.2m/s)$ whereas all other differences were significant $(p < 0.05)$. There was no effect of object size, $F(2, 94) = 0.29, \epsilon = 1.0, p = 0.75$, and no interaction, $F(6, 282) = 0.79, \epsilon = 0.91, p = 0.58$. This finding is in contrast to those of Hu et al. (1999) who found no influence of vision condition on peak velocity. However, Bradshaw and Watt (2002) reported a comparable decrease of velocity with increasing delay.

The relative time to peak wrist velocity was also affected by vision condition, $F(3, 141) = 54.57, \epsilon = 0.84, p < 0.001$. Post-hoc tests revealed significant differences for all pairwise comparisons (all $p < 0.05$). Again, no main effect of object size, $F(2,94) = 0.62, \epsilon = 0.94, p > 0.54$, and no interaction, $F(6,282) = 0.97, \epsilon = 0.82, p > 0.45$) were found.

2.2.3 Discussion

In this experiment we investigated the effect of introducing a delay on grasping kinematics. We were especially interested whether there is a difference between movements executed under full vision and movements in which the object is only visible until movement initiation. Additionally, we examined the effects of object visibility during the RT-interval which is supposed to be crucial for the kind of representation used during movement programming (Goodale et al., 2003, 2005).

Most of our main findings are in agreement with those of other studies examining the effects of reduced visual feedback during grasping (e.g., Wing et al., 1986; Jakobson & Goodale, 1991; Berthier et al., 1996; Churchill, Hopkins, Ronnqvist, & Vogt, 2000; Bradshaw & Watt, 2002; Schettino et al., 2003). With increased delay MGA was larger and occurred later in absolute time and earlier in relative time which in turn means that MT was prolonged. The transport component was also susceptible to the effect of delay such that peak velocity was reduced and occurred earlier in MT.

The contribution of the different delay conditions to the changes in the measured kinematic parameters differs, however, clearly from the predictions of the real-time view of action. Most kinematic parameters changed considerably between the CL and the OL-Move condition which is in contrast to the findings reported by Hu et al. (1999). Besides, we observed still a notable difference between the OL-Signal and the OL-Delay condition which would not be expected if a long-lasting ventral representation is used in these conditions, thereby also challenging the real-time view of action.

However, there is a simple explanation which can account for this observation. Looking at our data from the perspective of memory research it is reasonable to assume that the available information decays over time. During the period of stimulus presentation information about the stimulus is acquired. When the stimulus is physically removed from view this information begins to decay. It has been shown that exponential (e.g., Wickelgren, 1970; R. B. Anderson & Tweney, 1997) or power functions (e.g., J. R. Anderson & Schooler, 1991; Wixted & Ebbesen, 1997) are possible candidate functions to describe this decay for different kinds of information. Previous studies looking for decay functions of visuomotor information in aiming movements focused on the increase of movement variability after the removal of vision (e.g. Binsted, Rolheiser, & Chua, 2006; Rolheiser, Binsted, & Brownell, 2006). Rolheiser et al. (2006) reported a linear decay function for the hand movements and an immediate step decay for eye movements when vision of the target was prevented. Using a similar task Binsted et al. (2006) found a second–order increase in movement variability following the removal of the target object.

Figure 2.4 shows the means of MGA for our experiments, and for corresponding delay conditions reported by Hu et al. (1999) and Westwood et al. (2001) as a function of time of occlusion until MGA. Apparently, the increase of MGA due to longer durations of visual occlusion can be very well described by an exponential function in all studies. Thus, grasping seems to reflect an exponential decay of the visuomotor information rather than a sudden transition from one representation to the other as hypothesized by the real-time view of action. The information decay begins as soon as the object is removed from view reflected in the large increase in MGA between the CL and the OL-Move condition. In response to the decay of the visual information, participants increase their safety margin between fingers and the object (e.g., Wing et al., 1986; Jakobson & Goodale, 1991). This leads to an increase of the MGA which parallels the exponential decay of the visual information. As can be seen in Figure 4, this exponential relationship holds true for our Experiments 1 and 2 (the latter will be described in the following), but also for other studies using similar manipulations of the visual information: A recent study of Westwood et al. (2001) and the study of Hu et al. (1999) (although Hu measured only 3 data points, such that our exponential fit can only be tentative here).

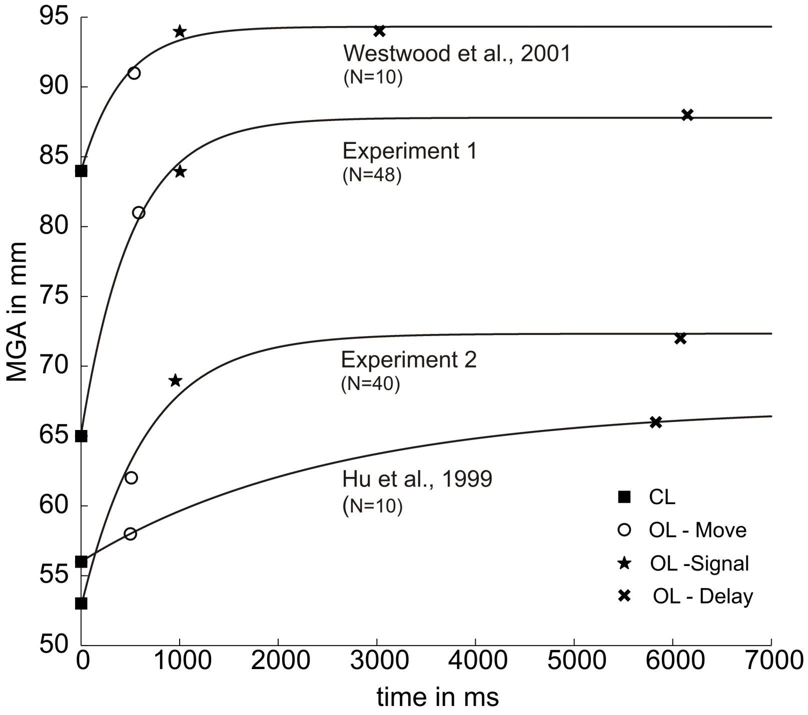


Figure 2.4: *Increase of MGA in corresponding delay conditions of Experiments 1, 2, the study of Hu et al. (1999), and the study of Westwood et al. (2001). The abscissa depicts the duration of the delay. That is, the time between closing of the goggles and the MGA (which is zero for the CL-condition, the absolute time of MGA in the OL-Move condition, the sum of absolute time to MGA and RT in the OL-Signal condition, and the sum of delay duration, RT, and time to MGA in the OL-Delay condition). Since RTs were not reported in the studies of Hu et al. (1999) and Westwood et al. (2001) we assumed a mean RT of 450 ms which is associated with cued prehension (Jakobson and Goodale, 1991). Exponential functions were fitted to these data points using a least square algorithm. The increase in MGA caused by the different delay durations is very well described by the exponential fit in all experiments.*

In conclusion, there is no reason to assume that during the RT-interval a transition to the use of a qualitatively different representation occurs. In fact, the observation that object visibility during the RT-interval influences movement kinematics can be attributed to a fast exponential decay of the visuomotor information.

Additionally, we had hypothesized that the slope of the function relating MGA to object size might change in the delay conditions. We found no evidence for this idea. The slope of the function seems to be relatively stable over the different conditions meaning that the scaling persists for all delay conditions. The increase in MGA after longer delays is thus an effect of a larger safety margin (larger intercept of the scaling function) between object and hand. This might indicate that the internal representation of the object size becomes more variable over time resulting in a loss of precision which is compensated by using a larger safety margin. The constant slope of the scaling function, however, suggests that there is no systematic bias in the estimation of object size after a delay.

In summary, the results show that the length of the delay between object presentation and movement initiation is important for action control since the visual information decays quickly. We showed that the decay of the visuomotor information can be well described by an exponential function and is therefore comparable to the decay found for other memory processes. In Experiment 2, we were interested in why Hu et al. (1999) found overall smaller effects of the delay (cf. Figure 2.4). One possibility might be that our stimuli were relatively small with a small contact surface (3x5 mm). Therefore, movements in our study might have required more accuracy (Zaal & Bootsma, 1993) than in the study of Hu et al. (1999) (contact surface: 4x4 cm). It might be that for more accurate movements more visual information is necessary. This idea seems also reasonable since in the study of Westwood et al. (2001), which reported similar changes in MGA between the CL and OL-Move condition, the stimuli had also small contact surfaces (4x4 mm). In Experiment 2 we wanted to examine whether movements which require less accuracy are affected in a similar way by the different delay conditions. Thus, we varied the accuracy demands of the task by changing object shape and using discs instead of bars.

2.3 Experiment 2

In this experiment we investigated whether the effects of the different delay conditions (same as in Experiment 1) on movement kinematics change when the accuracy demands of the movement were reduced by using discs instead of bars.

2.3.1 Methods

Participants Forty undergraduate and graduate students of the University of Giessen (13 males, 27 females, mean age = 23, SD = 4) participated in the experiment. They were paid 8 Euro per hour for participation. One experimental session lasted about 80 minutes. All participants were right-handed by self report and had normal or corrected-to-normal visual acuity. None of the participants took part in Experiment 1.

Stimuli and Procedure Apparatus and procedure were identical to Experiment 1. Three black discs with a diameter of 34, 36, or 38 mm and a thickness of 5 mm were used as target objects. Thus, the only differences to Experiment 1 were the shape and the size of the objects to be grasped.

2.3.2 Results

Data were analyzed using the same statistical procedures and dependent variables as in Experiment 1. The most important variable to detect effects of the different vision conditions was again MGA. The 4 (vision condition) x 3 (object size) repeated measures ANOVA revealed a significant main effect of vision condition, $F(3, 117) = 93.53, \epsilon = 0.83, p < 0.001$, and object size, $F(2, 78) = 54.33, \epsilon = 0.84, p < 0.001$. There was no significant interaction ($p = 0.62$). Figure 2.5a shows the increase in MGA for larger objects and for longer delays. The differences between the vision conditions are similar to those of Experiment 1 whereas the absolute size of MGA was smaller. Post-hoc tests confirmed significant differences between all vision conditions. Participants opened their hand in the OL-Move condition $9.2mm \pm 1.1mm$ wider than in the CL condition ($p < 0.001$). The difference between the OL-Move and the OL-Signal condition was $6.5mm \pm 0.9mm$ ($p < 0.001$) indicating a significant increase of MGA when vision during the RT-interval was unavailable.

The timing of MGA showed a somewhat different pattern than in Experiment 1 (cf. Fig. 2.5b). The significant main effect of vision condition on the time until MGA persisted, $F(3, 117) = 6.84, \epsilon = 0.84, p < 0.001$, indicating that MGA occurs later when vision is reduced. However, post-hoc tests revealed only significant differences between the CL and OL-Signal condition ($28ms \pm 11ms, p = 0.02$), the CL and the OL-Delay condition ($56ms \pm 14ms, p = 0.001$), and the OL-Move and OL-Delay condition ($28ms \pm 14ms, p = 0.001$). Thus, the CL and the OL-Move condition did not differ ($9ms \pm 14ms, p = 0.50$) which is in agreement with the findings of Hu et al. (1999). On the other hand, there was also no difference between the OL-Move and the OL-Signal condition ($18ms \pm 12ms, p = 0.14$) which would be expected if the RT-interval is critical for the kind of representation used. No effect of object size, $F(2, 78) = 2.02, \epsilon = 0.99, p = 0.14$, and no interaction, $F(6, 234) = 1.51, \epsilon = 0.79, p = 0.19$, were found on the timing of MGA.

The main effect of vision condition also holds for MT, $F(3, 117) = 32.51, \epsilon = 0.96, p < 0.001$ (cf. Fig. 2.5c). Vision conditions differed significantly from each other, $p \leq 0.001$, except for the CL and OL-Move conditions ($13ms \pm 20ms, p = 0.53$). Movements in the OL-Signal condition took on average $68ms \pm 18ms$ longer than in the OL-Move condition revealing a significant influence of object visibility during the RT-interval. No main effect of object size, $F(2, 78) = 2.04, \epsilon = 0.81, p = 0.15$, and no interaction, $F(6, 234) = 1.04, \epsilon = 0.50, p = 0.40$, on MT were found. The relative time to MGA in percent of movement time was also affected by the vision condition, $F(3, 117) = 16.60, \epsilon = 0.87, p < 0.001$ (cf. Fig. 2.5d) indicating that MGA occured earlier in MT when vision was reduced. As for MT, all pairwise comparisons were significant ($p \leq 0.01$) except for the difference between CL and OL-Move ($p = 0.73$). There was no main effect of object size, $F(2, 78) = 0.18, \epsilon =$

$0.98, p = 0.18$, and no interaction, $F(6, 234) = 1.25, \epsilon = 0.86, p = 0.29$.

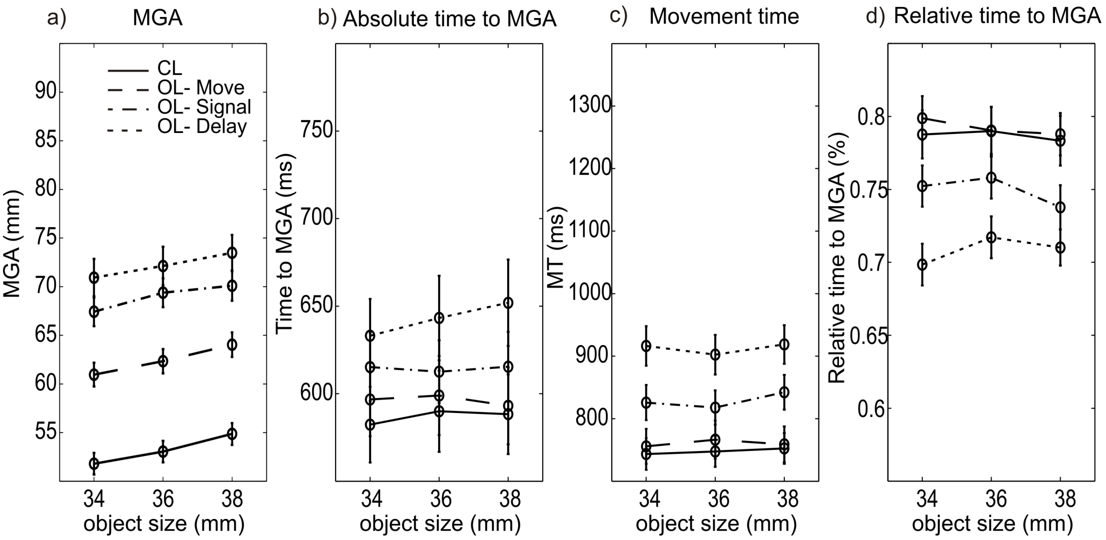


Figure 2.5: *Experiment 2: The effects of delay on: (a) MGA, (b) absolute time to MGA, (c) MT, and (d) relative time to MGA when grasping discs of three different diameters (34, 36 and 38 mm). All error bars depict ± 1 SEM (between subjects).*

As in Experiment 1 the slopes of the function relating MGA to physical size of the object were similar for all delay conditions: CL (0.77 ± 0.08), OL-Move (0.72 ± 0.13), OL-Signal (0.65 ± 0.14), and OL-Delay (0.66 ± 0.16). The repeated-measures ANOVA revealed no main effect of vision condition, $F(3, 117) = 0.20, \epsilon = 0.96, p = 0.89$. In comparison to Experiment 1 the slopes for the discs are overall slightly larger than for the bars.

For the transport component the same two parameters as for Experiment 1 were determined: peak wrist velocity and relative time to peak wrist velocity. As in the first Experiment peak wrist velocity decreased with increasing delay, $F(3, 117) = 11.46, \epsilon = 0.91, p < 0.001$. Post-hoc tests showed no significant difference between the CL and the OL-Move condition ($p = 0.39$), whereas all other differences were significant ($p < 0.05$). There was no effect of object size, $F(2, 78) = 0.43, \epsilon = 0.90, p = 0.43$, and no interaction, $F(6, 234) = 0.48, \epsilon = 0.86, p = 0.80$. Peak wrist velocity was reached earlier in MT when vision was reduced, $F(3, 117) =$

$21.92, \epsilon = 0.52, p < 0.001$. Post-hoc tests showed again significant differences for all pairwise comparisons ($p < 0.05$), except for the difference between CL and OL-Move ($p = 0.33$). No main effect of object size, $F(2, 78) = 2.09, \epsilon = 0.96, p > 0.54$, and no interaction, $F(6, 234) = 0.55, \epsilon = 0.86, p > 0.45$, were found.

2.3.3 Discussion

In this experiment we were interested in whether the different delay conditions have similar effects on kinematic parameters when the accuracy demands of the movement are reduced. Again, we were especially concerned with the differences between the CL and OL-Move condition and the changes which occur when object visibility is prevented during the RT-interval. For the size of MGA we observed a similar effect of delay as in Experiment 1. Participants opened their fingers wider in the OL-Move condition than in the CL condition which is again in contrast to the findings of Hu et al. (1999). As shown in Fig. 2.4 the increase in MGA with longer delays can very well described by an exponential function. In the other kinematic variables (relative and absolute time to MGA and MT), we observed no differences between the CL and OL-Move condition. The same was true for both measures of the transport component. The findings that MT and relative time to peak velocity of the wrist do not differ between the CL and OL-Move condition are in agreement with those of Hu et al. (1999). In contrast to our findings, Hu et al. (1999) did not find an effect of the delay on MT, timing of MGA and peak velocity of the wrist at all.

Overall, the kinematics of grasping movements directed to the discs were less affected by the introduction of a delay than the movements directed to the bars. Thus, the effects of delay on grasping kinematics seem to depend on the shape of the object and the resulting accuracy demands of the movement. Assuming that the visuomotor representation decays exponentially it seems reasonable that for movements which require less accuracy the decayed information is still sufficient to execute an accurate movement whereas movements which require more accuracy are stronger affected by the information decay. Therefore, one reason why Hu et al. (1999) detected even less differences between the different delay conditions might be that their stimuli had still much larger contact surfaces (4x4 cm) than our discs meaning that the representation needed not to be very accurate to execute an appropriate movement.

The comparison of Figure 2.3 and Figure 2.5 also reveals that, irrespective of the delay condition, for the discs MGA was smaller, occurred earlier in absolute time, and relatively later in MT than for the bars. Moreover, MT was shorter for the discs. These results are perfectly in agreement with Zaal and Bootsma (1993) who investigated the changes of kinematic parameters of grasping movements due to modified accuracy demands.

In Experiment 1 and 2 we examined the effects of reducing the visual information and increasing the memory demands in grasping. So far, we found evidence that kinematics were systematically influenced by longer delays and that the visuomotor information seems to decay exponentially. Moreover, the changes in movement kinematics due to the length of the delay depended on the accuracy demands of the movement to be executed. The most robust effect was an increase in MGA with increasing delay. This increase in MGA was thereby mainly caused by a larger safety margin of the grip. In Experiment 3 we wanted to examine the extent to which the grip aperture after a delay is comparable to the grip aperture induced by larger object sizes. That is, we wanted to test for qualitative differences between movements executed under full vision and movements executed without vision of the target object and after a delay. Therefore, we investigated grasping movements for a wide range of object sizes (1-10 cm) executed under full vision and compared them to the movements performed after a delay in Experiment 1. If delayed grasping uses qualitatively different information one would expect that the properties of the grip of delayed grasping movements differ from those of grasping movements executed under full vision. If, on the other side, participants only use a larger safety margin (because the visual information is decayed after a delay), then the grasping movements performed after the delay might be very similar to grasping movements performed under full vision, but to larger objects.

2.4 Experiment 3

In this experiment we wanted to examine to which extent the increase in MGA observed in the delay conditions of Experiment 1 and 2 is comparable to the increase in MGA induced by the use of larger object sizes. We were especially interested whether there is evidence for qualitative differences between movements executed under full vision and movements executed after a delay.

2.4.1 Methods

Participants Twenty undergraduate and graduate students of the University of Giessen (12 males, 8 females, mean age = 25, SD = 5) participated in the experiment. They were paid 8 Euro per hour for participation. One experimental session lasted about 60 minutes. All participants were right-handed by self report and had normal or corrected-to-normal visual acuity.

Stimuli and Procedure The apparatus and the procedure were identical to the previous experiments. But this time only the closed-loop condition was tested and a wider range of object sizes was used. After a preview period of 1 s participants grasped bars with a length of 1 cm up to 10 cm (in steps of 1 cm). The width and depth of the bars was the same as in Experiment 1 (5 mm and 3 mm). Each bar length was presented ten times in pseudo random order resulting in a total of 100 trials.

2.4.2 Results

Effects of object size

As expected MGA was significantly larger for larger object sizes, $F(9, 171) =$

$140, 10, \epsilon = 0.28, p < 0.001$ (cf. Fig. 2.6a). The linear regression analysis revealed that the slope of the function relating MGA to object size was 0.96 and remains linear over the whole range. Furthermore, MGA occurred later for larger objects, $F(9, 171) = 18.64, \epsilon = 0.32, p < 0.001$ (cf. Fig. 2.6b). As shown in Figure 2.6c, there was no influence of object size on MT, $F(9, 171) = 1.73, \epsilon = 0.58, p = 0.13$. Therefore, relative time to MGA was also later for larger objects, $F(9, 171) = 9.14, \epsilon = 0.55, p < 0.001$ (cf. Fig. 2.6d). Both measures of the transport component were unaffected by changes of object size: peak velocity of the wrist, $F(9, 171) = 1.08, \epsilon = 0.63, p = 0.38$, and relative time to peak wrist velocity, $F(9, 171) = 1.77, \epsilon = 0.62, p = 0.12$.

Aperture profiles: larger objects compared to longer delays

The main purpose of this experiment was to compare the aperture profiles resulting from grasping objects of different size in a CL-condition to the different aperture profiles caused by a delay (as measured in Experiment 1). We calculated the mean aperture profiles of the different conditions by averaging the data of all participants over time (every 5 ms; Optotrak sampled data with 200 Hz) from the beginning of the movement until the touch of the object. In Figure 2.7a-d the aperture profiles of the four delay conditions in Experiment 1 are shown. Each subplot shows the aperture profiles for the three different bar sizes used in Experiment 1 (39, 41, 43 mm, see the gray shaded lines). Each plot also contains the aperture profiles of Experiment 3 which fit best to the sizes of the aperture reached in the different delay conditions. The comparison of the aperture profiles in the CL-conditions of Experiment 1 and 3 shows that participants opened their hand wider in Experiment 1 to grasp a bar of similar size than in Experiment 3. This difference is likely due to the large between subject's variability in the experiments.

The comparison of the aperture profiles reveals a high similarity of the opening phase for all conditions. That is, if a delay is introduced then participants open

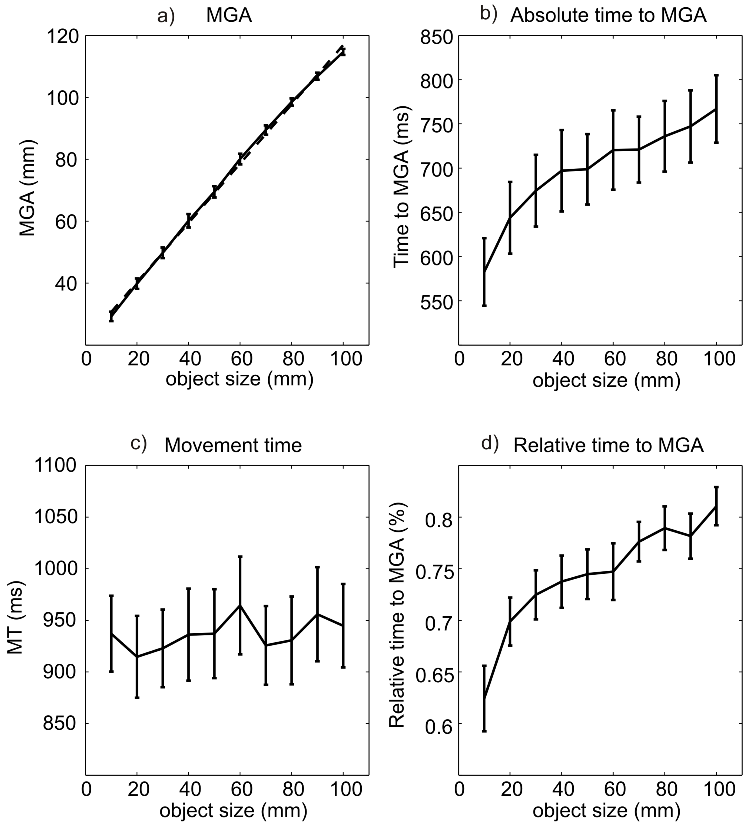


Figure 2.6: *Experiment 3: (a) MGA, (b) absolute time to MGA, (c) MT, and (d) relative time to MGA as a function of bar size (1-10 cm). All error bars depict ± 1 SEM (between subjects).*

their grip wider. They do this in a very similar way as if they plan to grasp a larger object. Only the latest phases of the movement differ because the physical sizes of the objects are different.

To examine the differences between the aperture profiles in more detail we calculated the velocity and acceleration profiles from the mean aperture profiles. These are shown in Figure 2.8. Again, the time course of aperture velocity and acceleration for the delay conditions resembles the profiles for the larger objects. The grip seems to evolve in three phases which are temporally relatively fixed: (a) a fast acceleration phase (about 80 ms), (b) a phase of relative constant velocity with an

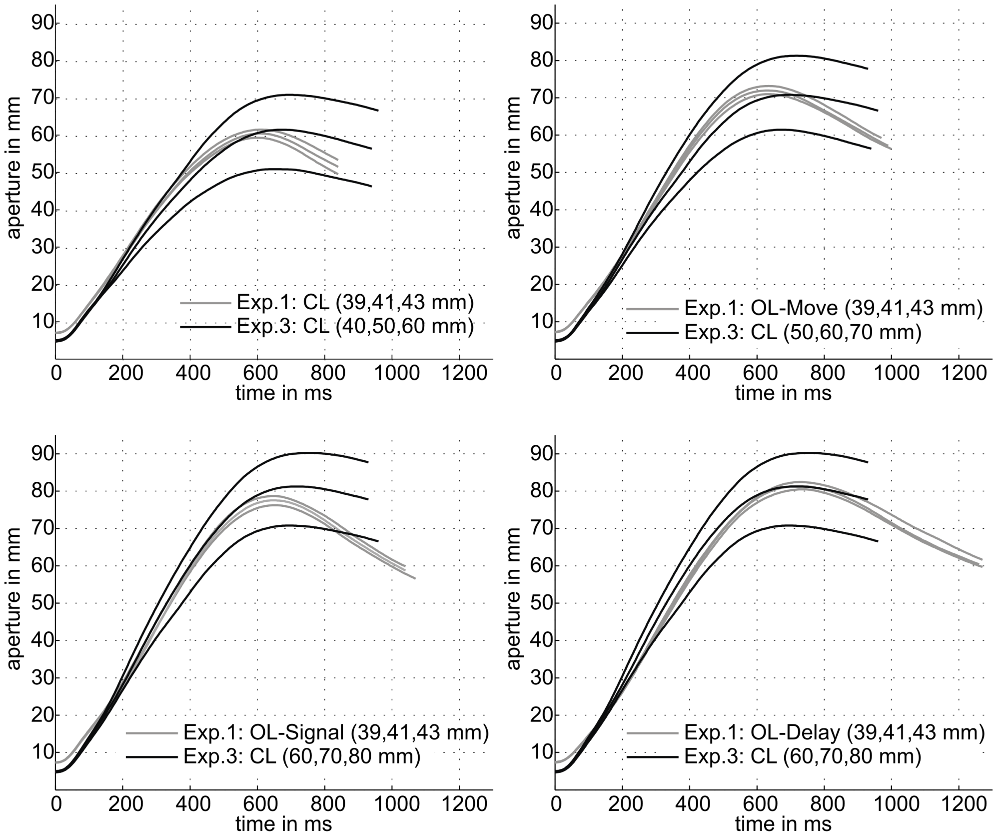


Figure 2.7: *Mean aperture profiles for the different delay conditions of Experiment 1 compared to the aperture profiles with a similar MGA when grasping larger objects under full vision in Experiment 3. The time course of the aperture in the delay conditions is comparable to the time course of the aperture directed to a larger object under full vision suggesting that there is no qualitative difference between these movements.*

acceleration of about zero (200-300 ms), and finally (c) a deceleration phase until the touch of the object. This pattern seems to be very stable no matter whether object size or delay are changed.

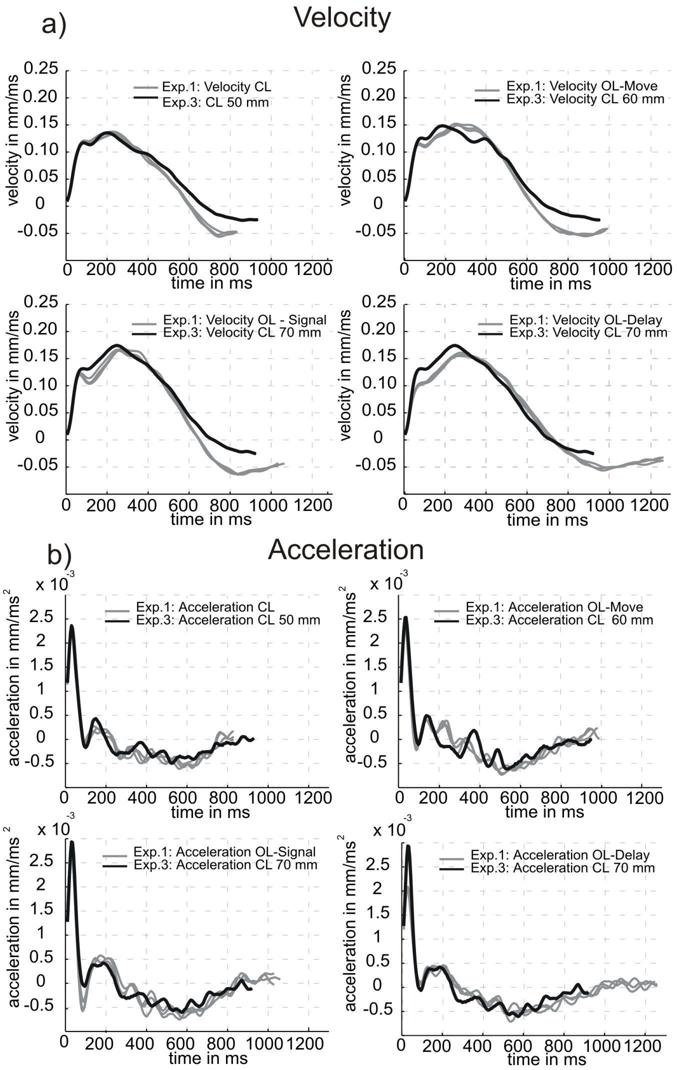


Figure 2.8: *Mean velocity and acceleration profiles (calculated from the mean aperture profiles of Fig. 2.7) of the different delay conditions of Experiment 1 compared to the velocity and acceleration profiles when grasping larger objects under full vision in Experiment 3.*

2.4.3 Discussion

In Experiment 3, we investigated the influence of object size on grasping kinematics under full vision and compared these effects to those of introducing a delay (Experiment 1). Our results corroborate the finding that MGA is linearly related to object size and that this relationship holds over a wide range of target sizes (e.g., Marteniuk et al., 1990). Moreover, the results on MGA also indicate that the smaller increase in MGA after longer delays in Experiment 1 and 2 cannot be attributed to a ceiling effect. In contrast to the results of Marteniuk et al. (1990) we found no effect of object size on MT. However, in their study the effects of changing object size were confounded with the effects of enlarging the contact surface of the object to grasp. It was already argued by Zaal and Bootsma (1993) that the negative relationship between object size and MT was the result of increasing the contact area of the stimuli and thus decreasing the accuracy demands rather than being a direct result of the change in object size. This interpretation is supported by our results.

Furthermore, we found no influence of object size on the transport component of the movement. This finding is in line with the conception of Jeannerod (1981, 1984). He describes the grasping movement as consisting of two coupled but relatively independent motor components: the transport component (carrying the hand to the object location) and the grasp component (shaping the hand in anticipation of the grasp). The manipulation of the intrinsic properties of the object, such as its size, affects only the grasp component but leaves the transport component relatively unaffected.

Finally, we compared the changes of the grasp component caused by enlarging the object size to those of introducing a delay. A comparison of the aperture time courses revealed a high similarity between the conditions. The opening phase of the aperture in the delay conditions is similar to the opening phase of grasping movements directed to larger objects under full vision. A closer look at the velocity and acceleration profiles of the grip aperture supports the similarity of the movements. Thus, analyzing the aperture profiles, we found no indication that grasping movements executed after a delay are qualitatively different from those executed under full vision.

2.5 General Discussion

In this study we investigated the influence of different delay conditions on grasping. In Experiment 1, we found the largest changes in movement kinematics between the full vision condition (CL) and the condition in which object visibility was only available during the RT-interval (OL-Move). Suppressing vision during the RT-interval and for a longer delay (5 s) had only a small additional effect. We showed that this finding can be very well described by an exponential decay of the visuomotor information used for movement execution. Figure 2.4 shows that the exponential decay function fits not only for our data but also for the data of Westwood et al. (2001) supporting the validity of this description. A similar exponential decay of the target representation is also reported in saccadic-eye-movement literature (e.g., Gnadt, Bracewell, & Andersen, 1991; Becker & Fuchs, 1969). Gnadt et al. (1991) showed that saccades to remembered targets show a considerable loss of accuracy within the first second following the offset of the visual target. After that period the distortion of the movement increased only slowly. Thus, the error of the movement increases quickly and remains than relatively stable for longer durations. This finding is in line with our results for grasping movements. Last but not least there is also evidence from memory research suggesting that it is reasonable to assume an exponential function to describe information decay adequately (e.g., Wickelgren, 1970; Loftus et al., 1992; R. B. Anderson & Tweney, 1997).

In Experiment 2 we showed that the effects of delay depend also on the properties of the stimuli used. If the movement requires less accuracy the differences between CL and OL movements were reduced. Therefore, our findings can provide an explanation for the small differences between CL and OL-Move condition found by Hu et al. (1999). We would argue that their results might be caused by the use of relatively large stimuli with large contact surfaces. Thus, the movements required only little accuracy and were less affected by occluding vision during movement execution and the resulting information decay. This interpretation seems also reasonable since they also did not find the usual effects on the timing of MGA and peak velocity of the movement after 5 s delay (e.g., Wing et al., 1986; Jakobson & Goodale, 1991; Berthier et al., 1996; Bradshaw & Watt, 2002). Besides, Hu et al. (1999) interpreted their findings as evidence for the real-time-view of action but did not test directly for the effects of suppressing vision during the RT-interval on movement kinematics. By investigating the effects of object visibility during the RT-interval directly, our study provides a stronger test of the predictions of the real-time hypothesis. To recapitulate, the "real-time" hypothesis of motor programming can only account for the changes in movement kinematic occurring between the OL-Move and the OL-Signal condition but not for changes between the CL and OL-Move (both assumed to be dorsal) and the OL-Signal and OL-Delay (both assumed to be ventral) condition. Therefore, our observation that object visibility during the movement strongly affects movement kinematics contradicts the real-time view of motor programming but it is in perfect agreement with earlier findings that suppressing visual feedback during movement execution results in slower movements, and wider MGAs which occur earlier in time (e.g. Wing et al., 1986; Jakobson & Goodale, 1991; Berthier et al., 1996; Churchill et al., 2000; Schettino et al., 2003).

In summary, our data show that there is no need to hypothesize the existence of two different representations: one highly accurate used for guiding and controlling movements in real-time (dorsal), and another one less accurate and thus not suitable to plan or control precise movements but which has to be used to execute movements when the target object is not visible (ventral). Data rather suggest that the visuomotor information decays over time. With longer delays the information becomes more imprecise. Thus, the uncertainty of the movement increases resulting in the observed changes of movement kinematics. These changes become especially obvious if the movement has to be very accurate. Experiment 3 provides further evidence that there seems to be no qualitative differences between movements executed after a delay and movements executed under full vision. Analyzing the aperture profiles suggests that grasping movements initiated after a delay are comparable to grasping movements directed to larger objects under full vision. This finding implies that increasing uncertainty due to fast information decay is compensated by the use of a larger safety margin during the grasp. In addition the slope of the function relating MGA to physical size is not affected by delay. We can combine both facts in a simple model: After a delay the information gets more unreliable (higher variability) but the delay does not introduce any bias in the size estimate (constant accuracy). The motor system reacts to this situation by choosing a larger MGA with a larger safety margin to compensate for the reduced reliability but leaves the slope relatively unchanged.

2.6 Conclusion

We investigated the properties of grasping movements directed to simple objects and executed after different delay durations. In accordance with earlier studies examining the role of visual feedback during movement execution (e.g. Wing et al., 1986; Jakobson & Goodale, 1991; Berthier et al., 1996; Churchill et al., 2000; Schettino et al., 2003) we found strong effects of preventing vision of the object and the hand during grasping on movement kinematics. Contrary to the real-time view of motor programming (e.g. Goodale et al., 2003, 2005) we found no indication for a transition from one to another representation guiding the movement. Our results suggest that the observed changes in grasping kinematics after a delay are due to an exponential decay of the visuomotor information over time (cf. Figure 2.4). This finding is in line with the description of information decay in the field of memory research and provides an interesting connection between fields of memory and motor actions. It might therefore be possible to use motor actions to investigate visual memory processes; thereby employing motor actions as a tool to study cognitive processes (as, for example, recently suggested Nakayama et al., 2007).

Chapter 3

Planning movements well in advance

Abstract

It has been suggested that the metrics of grasping movements directed to visible objects are controlled in real-time and are therefore unaffected by previous experience. We tested whether the properties of a visually presented distractor object influence the kinematics of a subsequent grasping movement performed under full vision. After viewing an elliptical distractor object in one of two different orientations participants grasped a target object, which was either the same object with the same orientation or a circular object without obvious orientation. When grasping the circular target, grip orientation was influenced by the orientation of the distractor. Moreover, as in classical visuomotor priming, grasping movements were initiated faster when distractor and target were identical. Results provide evidence that planning of visually guided grasping movements is influenced by prior perceptual experience, challenging the notion that metric aspects of grasping are controlled exclusively on the basis of real-time information.

3.1 Introduction

The anatomical and functional distinction between the dorsal and ventral streams of visual processing has been studied extensively (e.g., Ungerleider & Mishkin, 1982; Mishkin, Ungerleider, & Macko, 1983; Goodale & Milner, 1992; Milner & Goodale, 1995). However, the precise nature of this separation is still under debate. Milner and Goodale (1995) proposed that the distinction between the ventral and the dorsal stream corresponds to the distinction between perceptual representation (perception) and visuomotor control (action). According to their view, also known as the "two visual systems" hypothesis, the ventral stream is mainly involved in object identification and recognition whereas the dorsal stream mainly processes visual information for the control of actions (e.g., grasping).

One of the critical assumptions is that the two streams are assumed to process information on different time scales (Goodale, Jakobson, & Keillor, 1994; Milner et al., 2001; Rossetti, 1998). To be able to recognize objects, viewpoint independent information must be stored over a long time in the ventral stream. In contrast, spatial information in the dorsal stream that one relies on when interacting with the object only needs to be available for a few milliseconds since the relative positions of the observer and the goal object change all the time. Therefore, it is assumed that the information required for an action must be computed immediately before the beginning of the movement in real-time (Westwood & Goodale, 2003; Westwood et al., 2003). Consequently, whenever a movement is directed to a visible object (closed loop) the dorsal stream carries out fast, metrically accurate, visuomotor computations. The perceptual mechanisms of the ventral stream are only engaged in movement planning and control if the target is removed from view prior to response initiation (open loop). According to this "real-time view" of motor programming metric aspects of previously seen targets should not influence visually guided movements.

The fact that motor representations in the brain are activated by the mere presence of an object (e.g., Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Chao & Martin, 2000; Grèzes & Decety, 2002; Grèzes, Tucker, Armony, Ellis, & Passingham, 2003) and that previous movements influence goal-directed actions under some conditions (de Lussanet, Smeets, & Brenner, 2001; Jax & Rosenbaum, 2007) challenges such a clear functional distinction. Furthermore, it was shown by Haffenden and Goodale (2000a, 2002) that learned perceptual information can affect the kinematics of goal-directed actions as well. Visuomotor priming studies also seem to be inconsistent with the real-time view of motor programming (Craighero, Fadiga, Umilta, & Rizzolatti, 1996; Craighero, Fadiga, Rizzolatti, & Umiltà, 1998). In this paradigm, reaction times (RT) of grasping movements are shorter when grasping a target object which has congruent properties with a previously seen priming object than when grasping one that is incongruent with the prime. Craighero et al. (1996, 1998) concluded that prior visual information is used when performing a grasping movement. However, recent studies criticised this conclusion (Cant et al., 2005; Garofeanu et al., 2004; Goodale, Cant, & Króliczak, 2006). They argued that in the studies of Craighero et al. (1996, 1998) participants only received auditory information about the nature of the target object. Participants never saw the target stimulus they were supposed to grasp. Thus, the grasping movement was open-loop and had to be planned in advance. According to the real-time view of motor programming, the visual properties of a previously seen object, stored in the ventral stream, had to be used to perform those grasping movements. This would explain the priming effect, which is expected to occur when the metrics of the movement are derived from memory and not from direct visual information.

To resolve this potential problem, Cant et al. (2005) and Garofeanu et al. (2004) performed studies in which participants were able to see the target object during the programming phase of the movement or during the entire grasping movement. This ensured that the grasping movements towards the target could be programmed in real-time (dorsal stream) from direct visual input. No priming effect was found in these studies (Cant et al., 2005; Garofeanu et al., 2004). Cant et al. (2005)

interpreted these results as further evidence for the real-time view of motor programming and concluded that object orientation and position are object features which are always computed de novo by the visuomotor system when an action is required. In other words, the programming of movement parameters concerning the precise metrics of a closed-loop movement is assumed always to be carried out in real-time and not to be influenced by previous experience.

We think, however, that all studies discussed so far have a serious limitation. In all these studies, only RT was examined to determine whether the orientation of a previously shown object influences the movement towards a target object. However, RT might not be the best measure of information processing, because participants can start a movement before having analysed all information needed for that movement (van Sonderen & van der Gon, 1991). Therefore, in the study by Cant et al. (2005), participants could have started the grasping movement before specifying the exact orientation of the hand at the time of grasp and then adjusted the orientation of the hand on-line. Thus, measuring RT in a visuomotor priming paradigm might not reveal all use of prior information. The study of Jax and Rosenbaum (2007) is one example overcoming this "RT-limitation". They showed that the hand's path curvature of visually guided grasping movements was primed by the presence of an obstacle in previous trials, whereas no typical priming effects were found on RT.

In our study we tested directly whether visually guided grasping movements can use prior metric information. We examined the effect of a visually presented distractor object not only on the RT of a subsequent grasping movement, but also on kinematic variables, such as grip orientation. We presented distractor objects in a certain orientation before participants had to grasp either a similarly oriented target or a circular target with no obvious orientation. The target objects were fully visible during grasping such that, according to the real-time view of action, the dorsal stream should calculate the metric aspects of the object in real time. In consequence, kinematic variables such as the grip orientation should not show any influence of the distractor object if the real-time view of action is correct. If however, perception and memory are involved in the execution of visually guided grasping movements as proposed by other studies (e.g., Haffenden & Goodale, 2000a, 2002; Jax & Rosenbaum, 2007) then the orientation of the distractor object should influence the selected grip orientation when grasping the target.

3.2 Methods

Participants

Ten participants were recruited from within the Faculty of Human Movement Science of the Vrije Universiteit Amsterdam. All participants were right-handed by self report and had normal or corrected-to-normal visual acuity. The study was approved by the local ethics committee.

Apparatus and stimuli

Three cylindrical objects made of white plastic material served as distractor or target stimuli. One of the objects was a cylinder with a circular base with a diameter of 5 cm. The other two objects had an elliptical base (small: 5x2 cm, large: 7x5 cm; these were grasped along the 5 cm and 7 cm axes, respectively). All objects were 10 cm in height.

On each trial, a distractor and a target object were placed on a sliding carriage, each at one end in appropriately shaped cut-outs (Fig. 4.1). One of the objects was visible whereas the other was hidden from view. There was a surface at each side of the apparatus to occlude the view of the target when the distractor was presented and vice versa. To quickly change the object that the subject could see the sliding carriage was moved to the opposite side of the apparatus. This brought the other object to the same visible position. Each elliptical object could be placed in one of two orientations: 0° or 30° with respect to the participants' midline. The starting position of the hand was at the nearest corner of the surface above the right occluder (see Fig. 4.1).

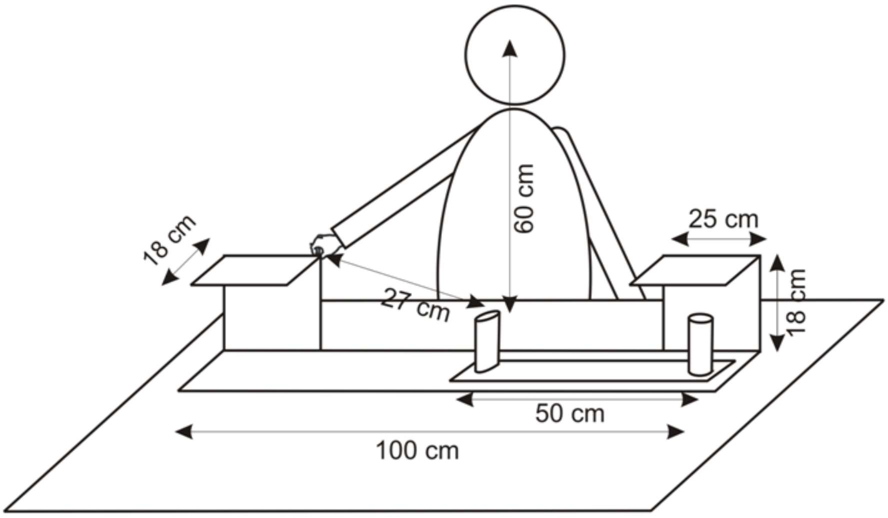


Figure 3.1: *Schematic drawing of the experimental setup (front view) showing a subject with the hand at the starting position.*

Trajectories of the grasping movements were recorded using a two camera Optotrak 3020 system at a sampling rate of 200 Hz. A small triangular plastic plate on which three infrared light-emitting diodes (IREDs) were mounted was attached to the nail of the thumb of the right hand, and a second one to the nail of the index finger. This enabled us to calculate the trajectories of the grasp positions from the trajectories of the three IREDs. To determine the grasping positions on the digits relative to the IREDs on the plastic plate a calibration trial, in which participants held an extra IRED between index finger and thumb, was recorded before the experiment started. In order to determine the moment in time at which the target object was lifted, an additional IRED was affixed to the target object. During the experiment participants wore liquid-crystal shutter glasses (Milgram, 1987), which could rapidly suppress vision by changing from a transparent to an opaque state.

Procedure

Participants stood in front of a table which was adjusted to the height of their hips. They looked down at the objects with a viewing distance of about 60 cm. Before starting the experiment, ten practice trials were executed for familiarisation with the task. At the beginning of each trial participants placed their hand at the starting position and the shutter glasses turned opaque. Subsequently, the experimenter placed a distractor and a target object on the sliding carriage. When the shutter glasses became transparent participants had to look at the distractor object, which was visible for 500 ms. Then the shutter glasses turned opaque again for an inter-stimulus interval (ISI) of 2 seconds. During the ISI the experimenter replaced the distractor by the target by moving the sliding carriage. Thus, the target object appeared at the same location as the previously shown distractor. After the ISI the shutter glasses became transparent again and at the same time an auditory signal cued the participants that they should grasp the target object. Participants were instructed to pick up the target object as quickly as possible. They were to grasp the upper half of the objects from the side using thumb and index finger (precision grip). They were to put the target object in front of themselves on the table and move their hand back to the starting position on top of the right occluder. The shutter glasses remained transparent during the entire grasping movement, so that participants had full vision of their hand and the target object.

Each of the three cylindrical objects (circular, small elliptical or big elliptical cylinder) of each orientation (0° or 30°) could serve as a distractor. The subsequent target was either the same elliptical object in the same orientation (control trials) or the circular cylinder (test trials) (for an overview of all conditions see Fig. 3.2). Each type of control trial was presented 25 times and each type of test trial 10 times. Control trials were presented more often than test trials in order to increase the probability that participants use the distractor object to plan the subsequent grasping movement. The condition in which the circular distractor was followed by the circular target was presented 10 times. This latter condition served as a baseline condition for grip orientation when normally grasping a circular cylinder. This results in a total of 150 trials that were presented in random order.

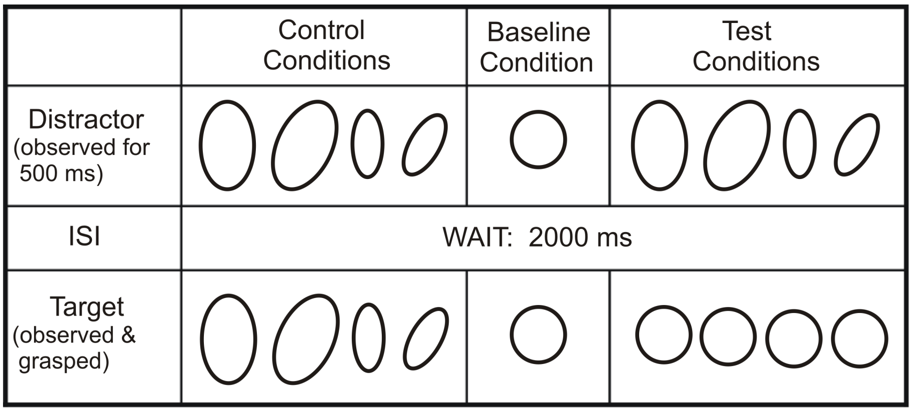


Figure 3.2: *Schematic representation of all nine combinations of distractor and target. The 0° stimuli were oriented sagitally and the 30° stimuli are rotated clockwise. Each test condition and the baseline condition were presented 10 times. The four control conditions were each presented 25 times.*

Data analysis

As the task primarily involved horizontal movements and only the horizontal orientation of the cylinders was manipulated, we only analysed the horizontal orientation of the hand. Grip orientation is defined as the angle of the horizontal projection of the line connecting the grasping positions of the index finger and the thumb (a sagittal line corresponds to a 0° orientation of the grip and a clockwise rotation is defined as positive). This angle was determined at different moments before and during the grasping movement.

Movement onset was defined by a velocity criterion. The first frame in which a digit exceeded a velocity threshold of 0.2 m/s was taken as movement onset. Movements were analysed until the marker mounted on the target object exceeded a velocity threshold of 0.2 m/s, which was considered as the lift-off of the object.

Reaction time (RT) is defined as the time between the auditory signal (and the target becoming visible) and movement onset. Movement time (MT) is defined as the time between movement onset and the lift-off of the target object. Maximum grip aperture (MGA) is defined as the maximum distance in 3D between the calculated grasp positions of the thumb and the index finger during the grasping movement.

Data of the test and control conditions were analysed using repeated-measure ANOVAs. Dependent variables were RT, MT, MGA and the orientation of the hand at different moments in time (one second before movement onset [ISI]; at movement onset; at MGA; and at lift-off of the target object). Values are presented as means ± standard errors of the means. A significance level of $\alpha = 0.05$ was used for all statistical analyses.

3.3 Results

Grip orientation in time

Our main interest was in the influence of the orientation of a distractor object on the grip orientation when subsequently grasping a target object. For this we analysed the test trials: trials in which the participants grasped the circular target object after having seen a small or large elliptical distractor object in a certain orientation (0° or 30°). A 2 (distractor orientation: 0°/30°) x 2 (distractor size: large/small) repeated-measures ANOVA was performed at four different moments in time (ISI, movement onset, moment of MGA and lift-off of the object). Each panel of figure 3.3 shows the grip orientation when the circular target object was grasped at one of those moments in time. During the ISI and at movement onset grip orientation was not affected significantly by the orientation of the previously seen distractor object, $F(1, 9) = 0.54, p = 0.48$ for ISI, and $F(1, 9) = 1.44, p = 0.26$ for movement onset. Grip orientation at MGA did depend on the orientation of the distractor object (23.3° ± 2.2° for distractor in 0° orientation and 28.9° ± 1.6°

for distractor in 30° orientation), $F(1,9) = 14.07, p = 0.01$. This effect on grip orientation was just as large at the moment the target object was lifted ($24.0° \pm 2.8°$ for distractor in 0° orientation and $29.8° \pm 2.2°$ for distractor in 30° orientation), $F(1,9) = 6.99, p = 0.03$. Thus, viewing a distractor object can influence the selected grip orientation when subsequently grasping a different object at the same position. None of the ANOVAs showed an effect of distractor size or an interaction between size and orientation (all $p > 0.43$).

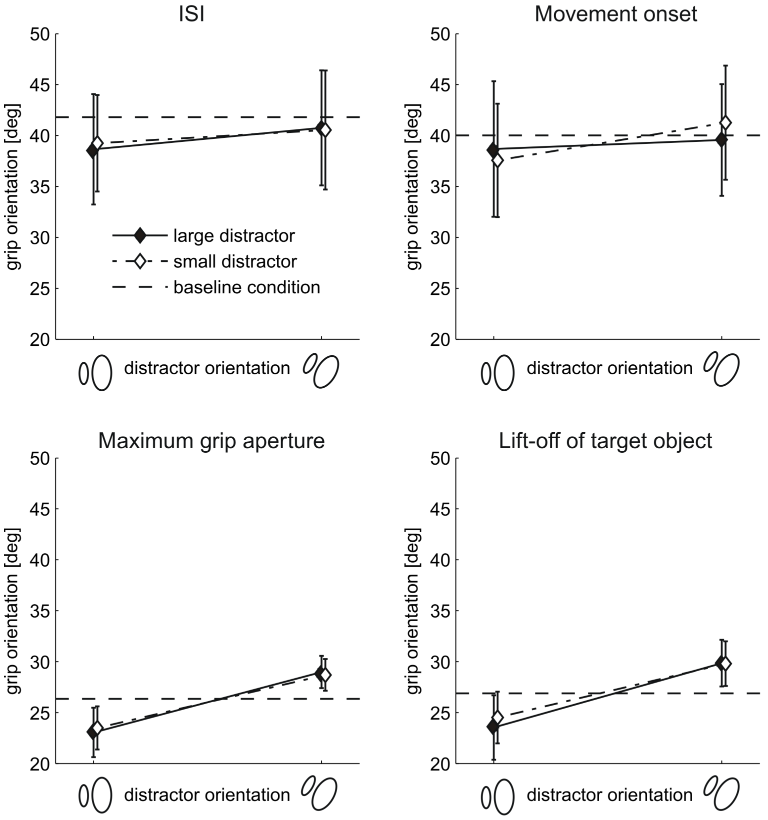


Figure 3.3: *Grip orientation (in degrees) when grasping the circular object (test trials) as a function of orientation and size of the distractor at four different moments in time: during the inter-stimulus interval (ISI), at movement onset, at maximum grip aperture (MGA) and at the moment of lift-off of the object. All error bars depict ± 1 SEM (between subjects).*

In trials in which the circular target object was grasped after having seen the same circular object as distractor (baseline trials), mean grip orientation was 26.4° ± 2.3° at maximum aperture and 26.9° ± 2.9° at the lift-off of the object. These values can be regarded as the preferred grip orientation when grasping a circular object (baseline). The orientation of the 0° distractor object is rotated counter-clockwise with respect to this baseline. Thus, the orientation of the 0° distractor is expected to affect the grip orientation of the target in a counter-clockwise direction. The 30° distractor is oriented more clockwise relative to the baseline and therefore should affect the grip in a clockwise direction. This prediction for the test trials is confirmed by our results. As expected grip orientation in the control trials (same size and orientation of distractor and target object) at MGA and at lift-off of the object is biased to the presented orientation (13.3° ± 1.1° for 0° orientation and 31.1° ± 0.9° for 30° orientation at MGA; 8.6° ± 1.0° for 0° orientation and 32.8° ± 1.0° for 30° orientation at lift-off of object).

Reaction and Movement Times

Reaction times shorter than 100 ms were excluded from the analysis. This occurred in fewer than 1% of the trials. In the visuomotor priming literature, RT of grasping movements are expected to be shorter if the target has congruent properties with the visually presented prime (e.g. Craighero et al., 1996, 1998). To examine whether the RTs are shorter in our control trials, in which the distractor is congruent with the target, than in our test trials, in which it is not, a 2 (distractor size: large/small) x 2 (distractor orientation: 0°/30°) x 2 (congruency: control/test trials) repeated-measures ANOVA was applied to the data. The baseline trials in which the circle served as both distractor and target object were not included in this analysis. As shown in Figure 3.4, participants had shorter RTs in the congruent control trials ($300ms \pm 25ms$) than in the incongruent test trials ($330ms \pm 23ms$), $F(1,9) = 58.61, p < 0.001$. The mean difference between the test and the control trials was 30 ms ± 4 ms. This finding is consistent with the visuomotor priming literature and confirms that the execution of grasping movements is affected by prior visual experience. There was no main effect of distractor size, $F(1,9) = 4.42, p = 0.07$ or distractor orientation, $F(1,9) = 0.15, p = 0.71$. Furthermore, no significant interactions were found (all $p > 0.07$).

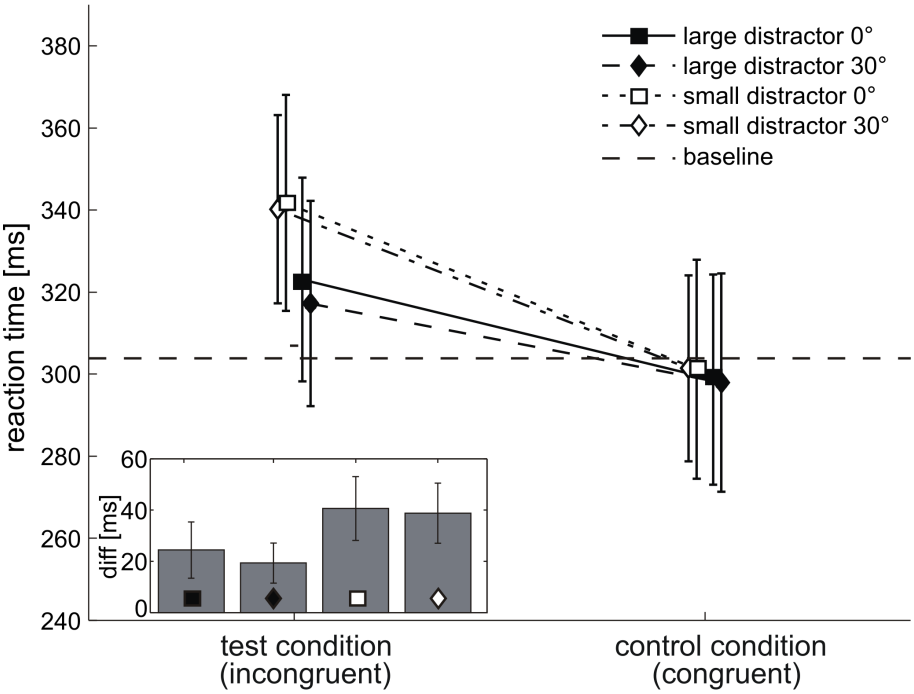


Figure 3.4: *Reaction times in test (incongruent) and control (congruent) trials. The inset shows the mean differences between the RTs for control and test trials for the different distractor objects. All error bars depict ± 1 SEM (between subjects).*

To analyse distractor effects on MT a similar 2 (distractor size: large/small) x 2 (distractor orientation: 0°/30°) x 2 (congruency: control/test trials) repeated-measures ANOVA was conducted. This test revealed no significant main effects or interactions (all $p > 0.13$). Thus, MT was unaffected by all presented distractor-target variations.

Maximum grip aperture

In order to investigate whether there is an influence of distractor size and orientation on MGA when grasping the target object, a 2 (distractor orientation: 0°/30°) x 2 (distractor size: large/small) repeated-measures ANOVA was carried out on the test trials. The ANOVA only revealed a main effect of distractor size, $F(1,9) = 10.99, p = 0.01$. Participants opened their hand wider when grasping the circular target object after having seen the small distractor object (MGA: $86.3mm \pm 2.8mm$) than they do after having seen the large distractor object ($84.0mm \pm 2.8mm$) (Figure 3.5, left panel). The mean value of MGA for the baseline condition (distractor and target object are circular) was $84.5mm \pm 2.2mm$. Since the size of the target object was always the same in the test trials, this finding demonstrates that the MGA is also influenced by the properties of a previously presented distractor object, although the direction of the effect was contrary to what one might expect. No main effect of distractor orientation and no interaction was found ($p > 0.55$).

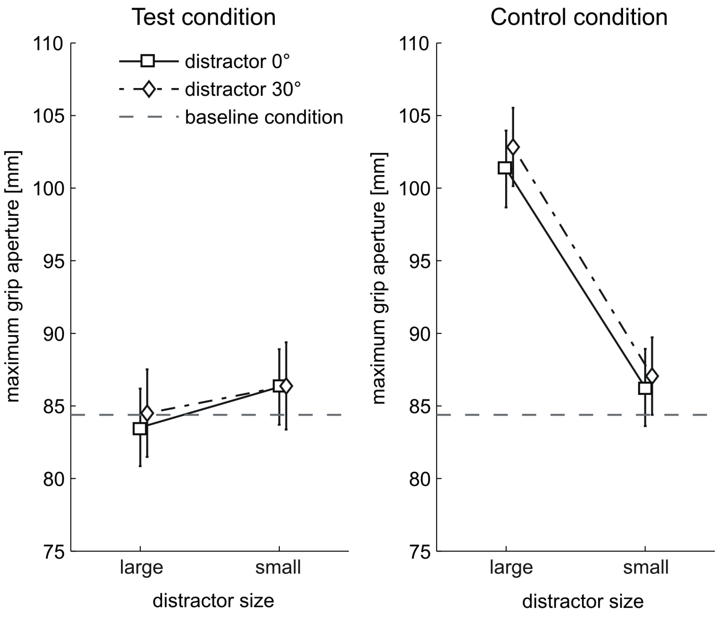


Figure 3.5: *Maximum grip aperture as a function of distractor size and orientation in test trials (left) in which the circular target object was grasped and in control trials (right) in which distractor and target object were identical. The dashed line represents the mean MGA when grasping the circular cylinder in the baseline condition. All error bars depict ± 1 SEM (between subjects).*

The right panel of Figure 3.5 shows the maximum grip aperture in the control trials (same size and orientation of distractor and target object). A 2 (distractor orientation: 0°/30°) x 2 (distractor size: large/small) repeated-measures ANOVA carried out on the control trials showed that, as expected, the larger target object was grasped with a larger MGA (small: $86.7mm \pm 2.6mm$; large: $102.1mm \pm 2.6mm$), $F(1,9) = 488.06, p < 0.001$. This is in agreement with the grasping literature showing an increase in MGA for larger objects (eg. Jeannerod, 1981, 1984; Smeets & Brenner, 1999). No effect of distractor orientation on MGA, $F(1,9) = 4.20, p = 0.07$ and no interaction ($p = 0.50$) was found.

3.4 Discussion

We investigated whether the planning and execution of a closed-loop grasping movement can be influenced by a previously presented distractor object. Grip orientation was affected by the orientation of the distractor object at the time of the MGA and at the moment the object was lifted. It was unaffected during the ISI and at movement onset, showing that the effect evolves during movement execution towards the target rather than the participants orienting their hand in response to the distractor during the interval before the target was presented. The influence of distractor orientation on grip orientation suggests that visually guided grasping can be planned well in advance, and that during this planning previous visual experience is taken into account (Haffenden & Goodale, 2000a, 2002). These results are inconsistent with the real-time view of motor programming (Westwood & Goodale, 2003; Westwood et al., 2003), whereby metric aspects of actions in response to visible targets are calculated in real-time, not using any stored information.

Beside the effect on grip orientation we also found that the RT was influenced by the presentation of the distractor object. RT is the standard variable used in visuomotor priming studies (Craighero et al., 1996, 1998; Garofeanu et al., 2004;

Cant et al., 2005). When the target was the same object in the same orientation as the distractor, RTs were shorter than when this was not so. These results are similar to the findings of Craighero et al. (1996, 1998), who also found a lower RT in congruent trials. According to the real-time view of motor programming, visually guided grasping should be unaffected by previous visual experience (Cant et al., 2005; Garofeanu et al., 2004) and information about the properties of the distractor should be "overwritten" by the visual presentation of the target object. Here we showed that visually guided grasping movements are affected even after an ISI of 2 s.

A difference between the present study and the priming studies of Cant et al. (2005) and Garofeanu et al. (2004) is that in our study the distractor provided information that was potentially useful for planning the movement, because in the control conditions (two-thirds of the trials) the orientation of the distractor and the target were identical, while in the test conditions the target had no obvious orientation. Therefore, one could think of a strategy in which participants always prepared for the orientation of the distractor. In the control condition this would result in an optimal preparation while the costs of a slightly unnatural grip orientation in the test condition would probably be low. This is in line with the arguments of Jax and Rosenbaum (2007) who concluded that in movement planning and control a balance of biomechanical and computational costs is accomplished. The computational advantage of pre-programming a movement based on the prime disappears if the prime provides no helpful information for the execution of the movement, so it is not self-evident from our results that the priming effects persist in such situations.

We also found an effect of distractor size on MGA in the test trials. Participants opened their hand wider when grasping a circular target after they saw a small distractor than when the same target was grasped after viewing a large distractor. There are two possible explanations for this unexpected result. First, in the framework of the grasping model of Smeets and Brenner (1999), the increase in MGA is due to the increased accuracy requirements for grasping objects with smaller contact surfaces. In our control condition we found a larger MGA for grasping the small elliptical object than for grasping the circular cylinder, although the grasp axis was the same length (in accordance with Cuijpers, Smeets, & Brenner, 2004). A transfer of this effect to the test condition suggests that the estimated accuracy demands of the movement are influenced by prior information. The second possibility is that the effect is due to the size contrast between distractor and target object: the target object is perceived as being larger when it is presented after a smaller distractor. Further research should clarify which of these alternatives is true. However, independent of which interpretation is true, the effect on MGA also contradicts the real-time view of motor programming and the idea that the information used at that stage is insusceptible to previous experience.

In conclusion, our study shows that fully visually guided movements can be influenced by the properties of a previously presented object, which contains relevant information about the target. This planning in advance is reflected in a change of movement parameters, in particular grip orientation, by the properties of the previously perceived object. Thus, our study provides further evidence that perception (Haffenden & Goodale, 2000a, 2002) and memory (de Lussanet et al., 2001; Jax & Rosenbaum, 2007) are involved in the execution of visually guided movements. This finding contradicts the real-time view of motor programming.

Chapter 4

Adaptive grasping: Corrective processes after perturbations of object size

Abstract

It was proposed that the adaptation of the grip to a new object size is achieved by reprogramming and substituting the initially planned motor program. We investigated corrective processes in grasping using a size perturbation paradigm. In three experiments we asked how grip adjustments are influenced by different perturbation times (early/late), the visibility of the moving hand, and different perturbation sizes (small/large). Results indicate that corrections are executed faster after late perturbations. The availability of visual information about the hand had only little effect on the corrections suggesting that feed-forward mechanisms are involved. Moreover, adjustments were mainly achieved by smooth changes of the aperture over time contradicting the assumption that a new movement is programmed and superimposed.

4.1 Introduction

Since the early investigations of Woodworth (1899) it is a central question in the field of motor control in which way visual information is used to control movement execution. Although, it is very reasonable that visual feedback improves goal–directed motor behavior such as pointing and grasping, it is still a matter of debate whether the execution of such movements relies on continuous visual control (e.g., Jeannerod, 1984; Connolly & Goodale, 1999; Schettino et al., 2003; Winges et al., 2003).

The most obvious approach to examine the importance of visual feedback for the execution of grasping movements is to remove vision of the hand during the movement and to examine the resulting changes in movement kinematics. In one of the first studies varying the amount of visual feedback Jeannerod (1984) reported that the kinematics of grasping movements executed under full vision (closed loop) were similar to those of movements without visual feedback about the moving hand (open loop). However, more recent studies revealed changes in some movement parameters when visual information was reduced. Connolly and Goodale (1999), for example, reported longer movement times caused by a longer acceleration and deceleration phase for grasping movements executed without vision of the hand but no influence on size and timing of maximum grip aperture (MGA). In contrast, many others (e.g., Jakobson & Goodale, 1991; Berthier et al., 1996; Churchill et al., 2000; Schettino et al., 2003) found larger MGAs which occurred earlier in movement time and a prolonged deceleration phase caused by a slower approach to the object. Thus, there is some evidence that vision of the moving limb makes an important contribution to the control of grasping movements.

On the other hand, there are also some properties of the grasp such as the scaling of aperture to object size and the gradual posturing of the fingers to object shape that remain relatively unaltered when vision of the hand is occluded (e.g., Jakobson & Goodale, 1991; Connolly & Goodale, 1999; Santello et al., 2002; Winges et al., 2003). This suggests that visual feedback of the hand is not essential to adjust the grasp to object properties. Jakobson and Goodale (1991) argued that the larger MGA observed for movements made without vision of the hand might be due to the fact that without visual information of the hand the fine-tune of the aperture is more difficult suggesting that a larger MGA and thus a larger "margin of error" is pre–programmed.

So far, studies provide evidence that visual information about the hand (when present) is used to program the movement and to improve the precision of the grasp (e.g., Jakobson & Goodale, 1991). Furthermore, most studies agree that visual feedback during grasping is especially important in the latter stages of the movement when the fingers close around the object. This observation is also in line with the proposition of Woodworth (1899). He stated that fast goal–directed movements consist of two successive phases: the "initial impulse" which is ballistic and thus uninfluenced by visual feedback is followed by the phase of "current control" using visual feedback in the end phase of the movement. Since Woodworth (1899) many researchers substantiated this view by showing that vision of the hand and the target becomes especially important in the final portions of the movement trajectory (e.g., Carlton, 1981; Chua & Elliott, 1993). It was argued that these corrections occurring in the end phase of the movement depend on a comparison between the position of the seen hand with respect to the target location (e.g., Carlton, 1981; Keele & Posner, 1968; Beggs & Howarth, 1972). Another reason why it seems reasonable that the first part of the movement is highly automatic and visual feedback is only used in the slow end phase of the movement is that feedback processes need time to become effective (visual processing delays c.f. Carlton, 1981). In a recent study Saunders and Knill (2003) showed that visual feedback about the moving hand is used continuously during the execution of reaching movements and not only in the end phase. They concluded that a fixed sensori–motor delay is the only limiting factor for visual feedback becoming effective. Furthermore, they propose that feed–forward models might also play a role in correcting movements on–line and to compensate for the delays in sensory feedback use (c.f. Desmurget & Grafton, 2000).

But, how is the movement controlled when the hand cannot be seen? One possibility that seems rather unlikely is that in these situations the whole movement is pre–programmed. This would also mean that in such situations no corrections can be accomplished. To examine this question in more detail some studies introduced a perturbation of the position of the target object during pointing movements and measured the resulting corrective processes (e.g. Komilis, Pélisson, & Prablanc, 1993; Prablanc, Pélisson, & Goodale, 1986; Prablanc & Martin, 1992; Goodale, Pélisson, & Prablanc, 1986). These studies show that corrective processes appear independently of visual feedback from the hand and even though participants were not aware of the perturbation. For example, Goodale et al. (1986) showed that pointing movements to an object that changed its position during the movement were successfully adjusted to the new target location when vision of the hand was suppressed challenging the notion that such movements are purely preprogrammed (Plamondon, 1995b, 1995a). From these findings it was concluded that non–visual information about the position of the hand like proprioceptive feedback and/or efference copies might play a major role in correcting goal–directed movements on–line (Goodale et al., 1986).

The perturbation studies mentioned so far dealt with pointing movements and the target perturbation was not noticed by the participants. Studies using the perturbation paradigm in grasping movements were so far mainly interested in the question of the (temporal) coupling of transport (carrying the hand to object's location) and manipulation (shaping the fingers in anticipation of the grasp) component (Jeannerod, 1981). Therefore, object position, related to the transport component of the movement and/or object size, related to the manipulation component of the movement were perturbed at the beginning of the movement. (e.g., Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991; Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Gentilucci, Chieffi, Scarpa, & Castiello, 1992; Castiello, Bennett, & Stelmach, 1993; Castiello, Bennett, & Chambers, 1998; Bock & Jüngling, 1999; Dubrowski, Bock, Carnahan, & Jüngling, 2002). Concerning the corrective response it was shown that changes of object size are associated with relatively long correction times (Paulignan, Jeannerod, et al., 1991: 330 ms) whereas corrections occurred relatively fast when object position was perturbed (Paulignan, MacKenzie, et al., 1991: 100 ms). To examine changes in grasping movements researchers mainly concentrated on the aperture profile especially the MGA which is known to be strongly correlated with object size and occurs well before the finger came in contact with the object (e.g., Jeannerod, 1984; Wing et al., 1986; Marteniuk et al., 1990; Smeets & Brenner, 1999). This pre–shaping of the hand is a highly stereotyped motor pattern which is largely pre–determined by object related visual input. If the object size is unpredictably changed a correction of the originally planned motor program is required. There are different possibilities how these corrections can be accomplished: the first motor program can be canceled and substituted by a new one, a second program can be superimposed to the first one, or the original motor program can be amended (c.f. Bock & Jüngling, 1999). Some studies reported a second peak in the grip aperture profile (”double peak pattern”) when the object size was increased during the movement (Paulignan, Jeannerod, et al., 1991; Castiello et al., 1993, 1998; Bennett & Castiello, 1995). This finding was interpreted as an indication that a second sub–movement is superimposed and that the motor program cannot be smoothly adjusted. However, studies that perturbed object size during grasping always introduced very large changes (e.g., Castiello et al. (1993): 0.7 to 8.0 cm; Paulignan, Jeannerod, et al. (1991): 1.5 to 6 cm; Dubrowski et al. (2002): 1.0 to 9.0 cm). Castiello et al. (1993) showed that this would normally lead to a change in the grasp type used (precision vs. whole hand grasp) rather than to an adjustment of the grip. To study correction processes in grasping in a more natural manner smaller changes have to be introduced.

Here, we were mainly interested in how much correction can be performed on–line and how visual feedback of the hand contributes to the adjustment of grasping movements to unexpected changes in object size. As described above visual feedback of the moving hand improves movement accuracy and reduces movement variability.

However, varying vision of the moving hand alone cannot answer the question in which way successful error correction is accomplished during the movement. Therefore, we utilized a perturbation paradigm. In 25% of the trials the size of the object to be grasped could become 1 cm larger or smaller. In contrast to other size perturbation studies we used much smaller changes in object size to examine movement corrections in a more natural manner. Furthermore, we sytemetically eliminated visual feedback about the hand between Experiment 1 and 2 (by using either a half–transparent mirror or a fully silvered mirror). By combining the size perturbation paradigm with the presence or absence of visual information about the hand we were able to determine the role of visual information in movement programming and execution on the one hand, and for successful on–line correction of the grasp on the other hand. Most of the studies using the size–perturbation paradigm in grasping introduced changes of object size by shifting the illumination from a small object to a large object to grasp and vice versa (e.g., Jeannerod, 1981; Paulignan, Jeannerod, et al., 1991; Castiello et al., 1993; Bennett & Castiello, 1995). It remains therefore unclear how well participants could see their hand during the movement execution and how vision of the hand contributes to a successful adjustment of the grasp.

To examine whether corrections are accomplished in a similar way during the whole movement we varied the occurrence of the size perturbations in movement time (early vs. late). Finally, we tested whether corrective processes are different when the required adjustments become more extensive (Experiment 3).

4.2 Experiment 1

In this experiment we investigated the effects of changing object size during the grasping movement at two different moments in time (early vs. late). We were mainly interested in how the movement is adjusted to an unexpected and small (±1 cm) size perturbation when participants were able to see their hand during movement execution.

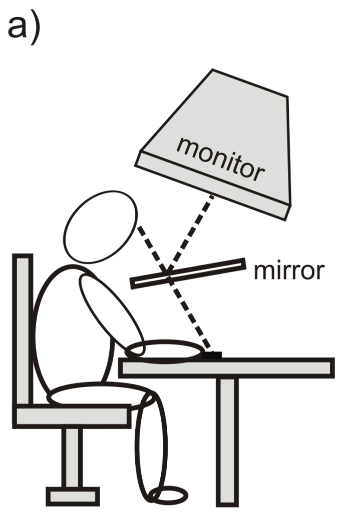
Methods

Participants

Twenty undergraduate and graduate students of the University of Giessen (mean age = 24, SD = 3) participated in the experiment. They were paid 8 Euro per hour for participation. All participants were right-handed by self report and had normal or corrected-to-normal visual acuity. One experimental session lasted about 90 minutes.

Apparatus and Stimuli

Participants sat on an adjustable chair using a chin rest to maintain a constant head position throughout the experiment. They looked down at a semi-transparent mirror (40 x 20 cm). The mirror was installed halfway between a monitor (Iiyama MA203DT 22”, refresh rate 85 Hz) displaying the virtual target objects and the table on which the real objects were placed. Thus, the virtual objects were projected at the level of the table top which served as working surface. The mirror setup was calibrated such that the contours of the 2-dimensional virtual object were aligned to the contours of the real object. Looking through the half-transparent mirror participants could see their hand and the virtual target object (cf. Figure 4.1a). The virtual target object was presented as a white rectangle on a black screen. The room was dimly lit to ensure that the real objects painted in black and presented on the black table could not be seen. This leads to the situation that participants reached and grasp for the virtual object below the mirror and met a real object at the expected location. Three black plastic bars of different lengths (45 mm, 55 mm, and 65 mm) but constant width (15 mm) and depth (15 mm) served as real stimuli.



b)

		perturbation direction	
		large-small (LS)	small-large (SL)
perturbation time	early	P65 - G55 P55 - G45	P45 - G55 P55 - G65
	late	P65 - G55 P55 - G45	P45 - G55 P55 - G65

Figure 4.1: *a) Schematic drawing of the experimental setup (side view). b) Overview of the different perturbation conditions in Experiment 1 and 2 (P indicates the size of the object size presented at the beginning of the movement, and G indicates the size of the object grasped after the perturbation had occurred. For example, P65 - G55 means that the object size presented was 65 mm. During the movement the object became 1 cm smaller matching 55 mm which corresponds to the size of the real object lying on the table).*

The trajectories of the finger movements were recorded by an Optotrak 3020 system (Northern Digital Incorporation, Waterloo, Ontario, Canada) at a sampling rate of 200 Hz. Light weight, small metal plates with three infrared light-emitting diodes (IREDs) were mounted to the nails of thumb and index finger of the right hand (using adhesive pastels: UHU-patafix, UHU GmbH, Bühl, Germany). Prior to the experiment a calibration procedure was used to measure the typical grasp points of the fingers relative to the three markers on the plate. Using mathematical rigid–body calculations, this allowed for an accurate calculation of the grasp points of index finger and thumb. An extra IRED was attached to the wrist to measure the transport component of the movement. In order to detect the exact moment when the target object was touched, an additional IRED was placed on the table left to the object and invisible to the Optotrak. Each object had a little mirror foil on the left side reflecting the signal of the IRED, which was registered by the Optotrak. As soon as the target bar was moved the Optotrak received a velocity signal indicating the exact time of contact with the stimulus (see also Franz et al., 2005 for this procedure).

Procedure

Participants started each trial with the index finger and thumb of the dominant right hand located at the starting position. The distance between starting position and object was 30 cm. Between all trials a different, randomly created white noise pattern was projected on the mirror. This allowed the experimenter to place the target object on the table below the mirror without being watched by the participant. Each trial started with the presentation of one out of three possible objects for a preview period of 1 s. Participants were instructed to look at the (virtually presented) object during this preview period but had to wait with their grasp until an auditory signal was given. In response to this auditory signal, participants grasped the bar along its major axis, lifted it, placed it halfway between object and starting position on the table, and moved their hand back to the starting position. Subsequently, the experimenter returned the bar and prepared the next trial. The virtual image of the object was extinguished when both fingers were in close vicinity to the target object (one finger was closer than 2 cm to the target position). No instructions were given as to speed of initiation and speed of the movement.

In 75% of the trials participants grasped the object which was presented during the preview period (non–perturbed trials). In the remaining 25% of the trials the virtually presented object changed its size during the movement (perturbed trials). The size of the perturbation was always + 1 cm (small–large; SL–perturbation) or - 1 cm (large–small; LS–perturbation). The 45 mm object could become 1 cm larger, the 55 mm object either 1 cm larger or 1 cm smaller, and the 65 mm object 1 cm smaller (cf. Figure 4.1b). In the end the virtually presented object always matched the size of the real object to be grasped. By using three different object sizes we could ensure that the medium sized object (55 mm) could either become 1 cm larger or 1 cm smaller. This extends the the size–perturbation procedure used in other studies in which the large object always gets small, and the small object always gets large (e.g., Paulignan, Jeannerod, et al., 1991; Castiello et al., 1993; Dubrowski et al., 2002). In addition, the size perturbation could occur at two different moments in time (defined by distances): (a) early: as soon as index finger or thumb had moved at least 2 cm away from the starting position or (b) late: after 2/3 of the movement distance. Each perturbation condition was presented six times resulting in a total of 48 perturbed trials. Each object size was also presented 48 times without any perturbation resulting in 144 non–perturbed trials. The presentation sequence of perturbed and non–perturbed trials was in random order. In all conditions participants were allowed 3 s to execute the movement (from the start signal until having removed the bar by at least 40 mm from its original position). If this time limit was exceeded, the trial was classified as an error and repeated later in the experiment at a random position.

Data Analysis

The finger trajectories were filtered off-line using a second-order Butterworth Filter employing a low-pass cut–off frequency of 15 Hz. Movement onset was defined by a velocity criterion. The first frame in which the index finger or the thumb exceeded a velocity threshold of 0.025 m/s was taken as movement onset. Reaction time (RT) was defined as the time between the auditory signal and movement onset. The touch of the object was also defined by a velocity signal given by the mirror attached to the objects. The first frame in which this signal exceeded a velocity threshold of 0.01 m/s was taken as the touch of the object. Movement time (MT) was defined as the time between movement onset and touch of the object. Furthermore, different parameters of the aperture profile (difference between index finger and thumb) were analyzed: MGA was defined as the maximum distance between thumb and index finger during MT. To characterize the transport component of the movement we determined peak velocity (PV), amplitude of peak velocity (APV) and time to peak deceleration (TPD) of the wrist marker.

Data were analyzed using repeated measures analysis of variance (ANOVA) and the Greenhouse-Geisser correction (Greenhouse & Geisser, 1959). This corrects for possible violations of the sphericity assumption in repeated measures data resulting in a more conservative testing. Values are presented as means ± standard errors of the mean. Post-hoc contrasts were carried out using Fisher's LSD (least significant difference) testing procedure. If not stated otherwise, a significance level of $\alpha = 0.05$ was used for the statistical analyses.

Results

MGA

We examined the changes of kinematic parameters due to small and unexpected changes in object size during movement execution. The main variable we were interested in was MGA which is known to be strongly correlated with object size (c.f. Smeets & Brenner, 1999). A repeated–measures ANOVA on the non–perturbed trials showed that, as expected, the larger objects were grasped with a larger MGA, $F(2,38) = 297.5$, $\epsilon = 0.7$, $p < 0.001$, (cf. the black lines in Figure 4.2). The slope of the function relating MGA to object size was 0.65 ± 0.04.

More interesting are, however, the differences between the different perturbation

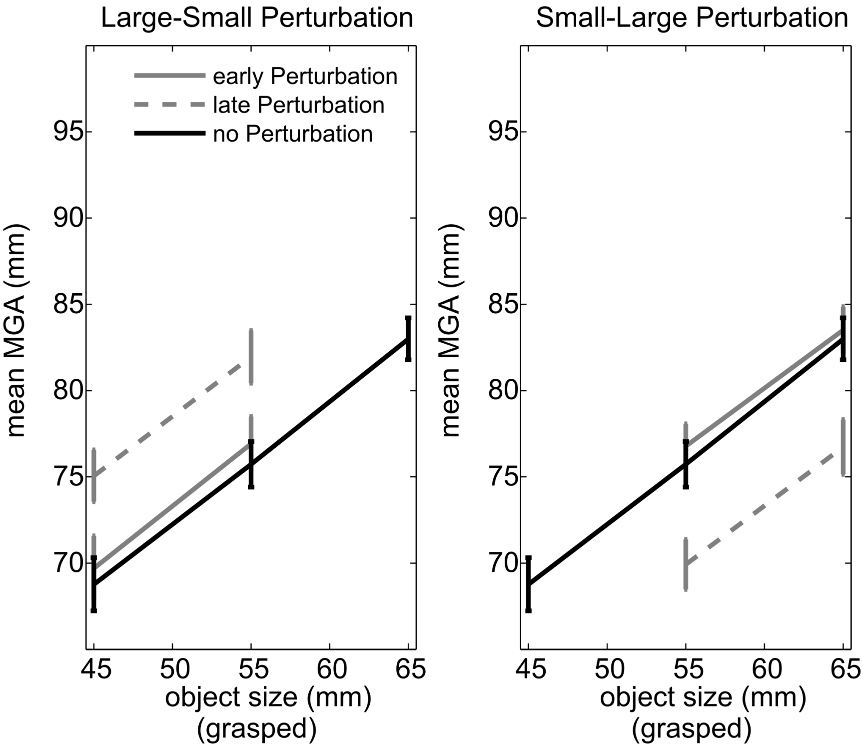


Figure 4.2: *Experiment 1: Maximum grip aperture as a function of grasped object size and perturbation time. The left panel shows the perturbation trials in which the object became 1 cm smaller and the right panel shows the perturbation in which the object became 1 cm larger. The black lines represent MGA in the non–perturbed trials. All error bars depict ± 1 SEM (between subjects).*

conditions. Figure 4.2 shows that after an early perturbation the MGA was relatively well adapted to the new size of the object whereas this adaption did not occur after a late perturbation. This observation was statistically confirmed by a 2 (object size) x 3 (perturbation type: early, late, none) repeated–measures ANOVA conducted separately for LS–trials and SL–trials. Firstly, we analyzed the factor perturbation type by selecting the perturbation conditions in which the size of the object actually grasped (the second object size displayed) was the same as in the no–perturbation condition (cf. Figure 4.2). This analysis revealed a significant effect of perturbation type for the LS–trials, $F(2,38) = 98.28$, $\epsilon = 0.97$, $p < 0.001$, as well as the SL–trials,

F(2,38) = 96.29, $\epsilon = 0.58$, $p < 0.001$. Pairwise comparisons showed that the MGA in the early perturbation conditions did not differ significantly from the MGA in the no–perturbation conditions: The difference was $1.0mm \pm 0.5mm$ ($p = .06$) in the LS–condition, and $0.8mm \pm 0.4mm$ ($p = .07$) in the SL–conditions. In contrast, the MGA in the LS late perturbation conditions was significantly larger compared to the non–perturbed trials: $6.3mm \pm 0.5mm$ ($p < .001$) and significantly smaller in the SL late perturbation conditions $6.0mm \pm 0.5mm$ ($p < .001$). These results confirm that after an early perturbation, but not after a late perturbation, the MGA was adapted to the new object size. There was a significant effect of object size in all analyzes (all $p < 0.001$) but no interactions (all $p > .76$).

In the complementary analysis we selected the perturbation–trials in which the size of the object displayed first matched the size of the object grasped in the no–perturbation condition respectively and conducted the same 2 (object size) x 3 (perturbation type: early, late, none) ANOVA for LS and SL conditions. In this case we expected that the size of the MGA in the late perturbation trials does not differ from the MGA in the no–perturbation trials since no correction had occurred. The analysis revealed again a significant effect of perturbation type for the LS–conditions, F(2,38) = 78.73, $\epsilon = 0.72$, $p < 0.001$, as well as for the SL–conditions, F(2,38) = 103.10, $\epsilon = 0.82$, $p < 0.001$. Post-hoc comparisons confirmed that in the LS–conditions MGA in the late perturbation conditions did not differ from the MGA in the no–perturbation conditions, $0.9mm \pm 0.4mm$ ($p = 0.06$), whereas MGA was significantly smaller in the early perturbation conditions, $6.1mm \pm 0.6mm$ ($p < 0.001$). For the SL–conditions the MGA in the early perturbation condition was $7.9mm \pm 0.6mm, (p < 0.001)$ larger than in the corresponding no–perturbation conditions. The difference between late perturbation and no–perturbation conditions was also significant, $1.1mm \pm 0.5mm, (p = 0.03)$ indicating the MGA was larger in the late perturbation conditions.

Aperture profiles

By investigating the size of MGA we found evidence that early perturbations are successfully corrected during the movement. However, so far we cannot determine the particular mechanisms and the time course by which these corrections are accomplished. Therefore, we examined the aperture profiles in more detail. Mean aperture profiles of the different conditions were calculated by averaging the data of all participants over time (every 5 ms; Optotrak sampled data with 200 Hz) from the beginning of the movement (RT). In Figure 4.3 the mean aperture profiles of the different perturbation conditions are shown. The visual inspection of the aperture time courses reveals that after the perturbation had occurred the aperture follows relatively long the time course of the aperture profile of the object size displayed first in the corresponding non–perturbed condition.

To quantify this observation we calculated the difference of the mean non–perturbed aperture profile and the mean perturbed aperture profile, starting with the same object size. Then t-tests were calculated at each time point. If the difference between the perturbed and non–perturbed aperture profile became significant ($\alpha = 0.01$, the higher alpha level was chosen because of the multiple testing procedure) this was taken as the moment the correction occurred. The correction times are also shown in Figure 4.3. After an early perturbation we found correction times of about 295 ms for the LS–perturbation condition, and 262 ms for the SL–perturbation condition respectively. These correction times are in a similar range as those reported in other size perturbation experiments (e.g., Paulignan, Jeannerod, et al., 1991; Bock & Jüngling, 1999; Dubrowski et al., 2002) and are also comparable to the RTs needed to initiate goal–directed movements (c.f. Bock & Jüngling, 1999). Regarding the late perturbation conditions the correction times found were considerably shorter: 166 ms in the LS–perturbation condition and 169 ms in the SL–perturbation condition. This finding suggests that corrections can be faster incorporated during the final phase of the movement.

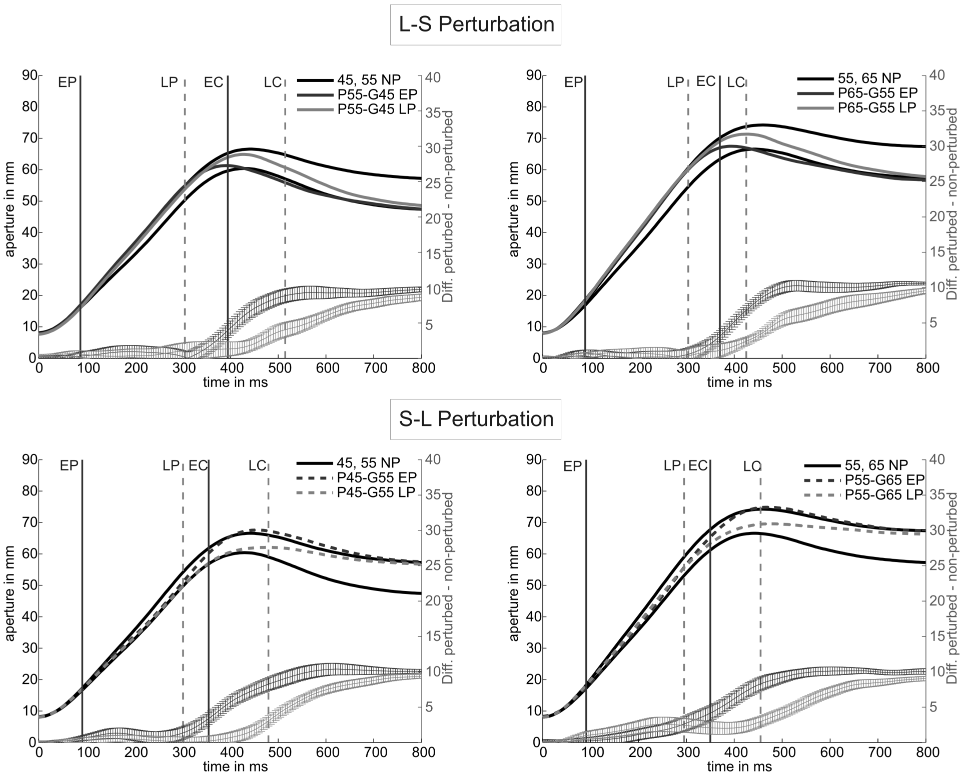


Figure 4.3: *Experiment 1: Mean aperture profiles for the different perturbation conditions. The solid black lines represent the aperture profiles in the non–perturbed trials. The vertical lines depict the perturbation and correction times in the different conditions (EP: early perturbation time, LP: late perturbation time, EC: early correction time, LC: late correction time). The lines with the error bars depict the mean differences between perturbed and corresponding non–perturbed aperture profiles which were used to calculate correction times (more information is given in the text).*

Double–Peak Pattern

It has repeatedly been reported that changing the size of an object during the movement results in a "double–peak pattern" of the aperture profile (e.g., Paulignan, Jeannerod, et al., 1991; Castiello et al., 1993, 1998; Bennett & Castiello, 1995). That is, when an object becomes larger the grip aperture first peaks to the size of the small object and then increases to the size corresponding to the larger object. This finding was taken as indication that a second sub–movement is programmed and superimposed on the original planned movement program. However, the occurrence of this pattern was reported exclusively by showing representative single subject data. Here we examined the "double–peak" pattern in a more systematical way. Therefore, we differentiated the aperture profile for each participant and each trial until MGA was reached. Whenever there was a change in the algebraic sign from plus to minus a local maximum was detected indicating a second peak in the aperture profile. Figure 4.4 shows the percentage of double–peaks averaged over all participants in all experimental conditions. A repeated–measures ANOVA over all five conditions did not reveal an effect of condition, $F(4, 76) = 0.74, \epsilon = 0.47, p = 0.54$. By determining the number of double–peaks also in the non–perturbed trials it turned out that some participants often show double–peaks in both, perturbed and non–perturbed trials whereas others did not show double–peaks at all. This observation was confirmed quantitatively by a bivariate correlation showing that all correlation coefficients between the number of double–peaks in the no–perturbation condition and the four perturbation conditions were higher than $r = .85$, and significant (all $p < .001$).

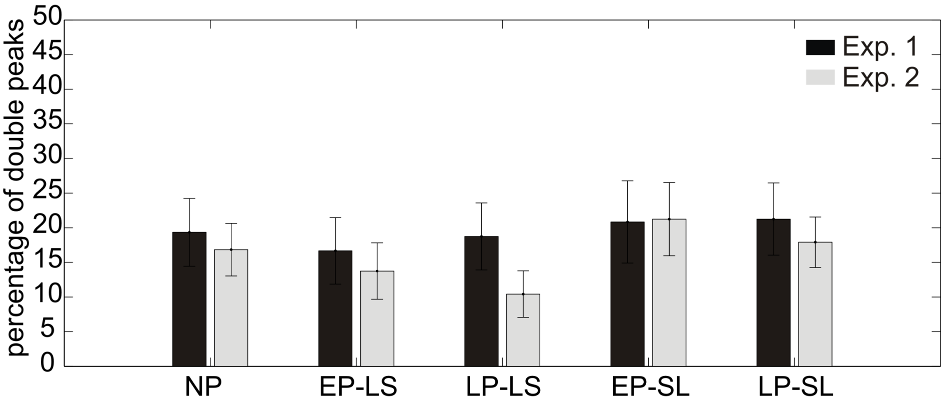


Figure 4.4: *Mean percentage of double–peaks for the different perturbation conditions in Experiment 1 and 2. In Experiment 1 participants were able to see their hand during movement execution whereas in Experiment 2 vision of the hand was suppressed. All error bars depict ± 1 SEM (between subjects).*

Transport component

The wrist IRED was used to analyze the transport component of the grasping movement. Wrist movements are known to have a single peak and a bell–shaped velocity profile and can thus be well characterized by measuring the amplitude of peak velocity (APV), the time to peak velocity (TPV) and the time to peak deceleration (TPD) (e.g., Paulignan, MacKenzie, et al., 1991; Paulignan, Jeannerod, et al., 1991).

To test for the effect of object size perturbation on the wrist parameters we averaged the trials in which the object became smaller (LS–trials: containing all P55-G45 and P65-G55 trials) and the trials in which the object became larger (SL–trials: containing all P45-G55 and P55-G65 trials) and compared them to the average of the non–perturbed trials respectively (mean of all G55 and G65 non–perturbed trials compared to the LS average, and mean of all G45 and G55 non–perturbed trials compared to the SL average). Finally, a repeated–measures ANOVA with the factor perturbation type (early, late, none) was separately applied to the LS and the SL conditions.

LS–Perturbation: The only significant effect on the values of the wrist kinematic landmarks was found for MT, $F(2{,}38) = 8.75$, $\epsilon = 0.97$, $p = 0.001$. Post–hoc tests revealed that movements in the late perturbation conditions took longer than in the non–perturbed and early perturbed conditions (Table 1). All other parameters characterizing the transport component of the movement were uninfluenced by the changes of object size.

SL–Perturbation: No effect on MT, TPV, and APV was found for the conditions in which the object became larger (Table 1). The TPD was affected by the different conditions indicating that TPD occurred earlier in the late perturbation conditions, $F(2{,}38) = 4.14$, $\epsilon = 0.77$, $p = 0.04$.

	MT	TPV	APV	TPD
non-perturbed (L)	690 (41)	245 (12)	0.92 (0.03)	396 (18)
LS early	712 (45)	245 (12)	0.92 (0.03)	399 (17)
LS late	737 (48)	245 (12)	0.93 (0.03)	401 (18)
non-perturbed (S)	713 (44)	244 (12)	0.92 (0.02)	398 (17)
SL early	707 (42)	243 (12)	0.92 (0.03)	399 (17)
SL late	686 (41)	241 (12)	0.93 (0.03)	387 (17)

Note. Standard errors are given in parentheses.

Table 1: Kinematic characteristics of the transport component during LS–perturbed and SL–perturbed trials (hand visible during movement execution). MT: movement time (ms); TPV: time to peak velocity (ms); APV: amplitude of peak velocity (mm/ms); TPD: time to peak deceleration (ms).

In summary, wrist kinematics were extremely stable and only little affected by changes in object size. This finding is in accordance with other studies also observing no consistent changes in the transport component when the object size was perturbed during grasping (Jeannerod, 1981; Paulignan, Jeannerod, et al., 1991).

Discussion

In this experiment we studied the adaptability of grasping movements. In particular we wanted to know how quickly the motor system adapts to changes in object size and in which way the necessary corrections are accomplished. To this end we applied a size–perturbation paradigm introducing small changes of object size ($\pm 1cm$) at two different moments in time (early/late). The size–perturbation required an adjustment of the grip, mainly characterized by a rescaling of the aperture, in order to grasp the object successfully.

In accordance with other studies examining the effect of size perturbations on grasping we found that grip formation was strongly affected by object size and the introduced perturbations whereas the transport component remained relatively uninfluenced (Jeannerod, 1981; Paulignan, Jeannerod, et al., 1991). Our findings suggest that the adaptation of the grip to the new object size is achieved by smooth changes in the aperture over time. This was confirmed by a single grip opening of the fingers in most of the trials. The result is in contrast to other studies reporting a double–peak pattern in the aperture profile when the object to grasp became larger (e.g. Paulignan, Jeannerod, et al., 1991; Castiello et al., 1993). It was argued that this second peak in the aperture indicates a re–programming of the movement. There might be two reasons why we did not find this pattern in response to SL–perturbations: Firstly, we used much smaller perturbations of object size ($\pm 1cm$ compared to $\pm 7.3cm$ in the study of Castiello et al. (1993); or $\pm 4.5cm$ in the study of Paulignan, Jeannerod, et al. (1991)) suggesting that smaller corrections might be accomplished differently. For example, Roy, Paulignan, Meunier, and Boussaoud (2006) who investigated the effects of size perturbation in monkeys also reported a smooth reorganization of the grip when the object size was changed by just 1 cm. Secondly, by using the non–perturbed condition as baseline we found that the double–peak pattern occurs relatively independent of the perturbation condition. The high correlations between the number of double–peaks in non–perturbed trials and the number of double–peaks in the perturbed trials led us to the assumption that double–peaks represent a individual movement pattern rather than an evidence for movement reprogramming. This notion is further supported by the fact that Paulignan, Jeannerod, et al. (1991) found double–peaks only for three out of five subjects and Castiello et al. (1993) reported double–peaks only for half of the subjects whereas the other half showed a smooth adjustment from the small to the large aperture. Furthermore, in these studies it was only looked for the occurrence of double–peaks in the perturbed conditions but not in the non–perturbed trials.

Regarding the time course of the corrective movements after early perturbations, we found correction times that are similar to those reported in recent studies (e.g., Bock & Jüngling, 1999; Dubrowski et al., 2002). However, when the size perturbation occurred later during the movement the correction times were about 100 ms shorter. This finding is in line with the proposition of Woodworth (1899) that goal–directed movements consist of two successive phases: the initial impulse which is entirely ballistic and the current control in which errors of the initial movement trajectory are corrected. This second phase is assumed to depend on visual and proprioceptive information about the position of the end–effector in relation to the target. In our experiment, the early perturbation occurred on average 90 ms after movement initiation during the acceleration phase of the fingers (c.f. Hesse & Franz, submitted). Assuming that in this early phase newly incoming visual information cannot be integrated immediately in the ongoing movement, corrections are not carried out until the corrective phase of the movement. In contrast the late perturbation occurred approximately 300 ms after the movement initiation when the fingers already begin to decelerate. Supposed that the movement is already in the corrective phase the incoming visual information can directly be used to modify the grip resulting in shorter correction times. Thus, the grasping movement seems also to be a combination of preplanned and current control processes meaning that (visual) information can be used in the latter half of the ongoing movement to correct for possible errors. In contrast to the findings of Glover, Miall, and Rushworth (2005) we did not find that adjustments to SL–perurbations are initiated earlier than to LS–perturbations. This difference might be again due to the much smaller perturbations used in our study than in the study of Glover et al. (2005) ($\pm 5cm$).

However, so far we cannot determine the importance of visual feedback about the moving hand relative to the target for on–line adjustments at the end of the movement. There is evidence from pointing studies that correction characteristics are similar with and without vision of the moving hand (e.g., Goodale et al., 1986; Prablanc & Martin, 1992; Komilis et al., 1993). However, in these studies participants were unaware of the target perturbations. To examine the role of visual information about the hand for correcting the grip in response to an object size perturbation which is consciously perceived we did exactly the same experiment but prevented vision of the hand when grasping the object.

4.3 Experiment 2

In this Experiment we used exactly the same perturbation conditions as in Experiment 1. The only difference was that this time a fully–silvered mirror was installed such that the participants had no visual information about their moving hand during movement execution.

Methods

Participants

Twenty undergraduate and graduate students of the University of Giessen (mean age = 25, SD = 4) participated in the experiment. They were paid 8 Euro per hour for participation. All participants were right-handed by self report and had normal or corrected-to-normal visual acuity. One experimental session lasted about 90 minutes.

Stimuli and Procedure

Apparatus and procedure were identical to Experiment 1. The only differences to Experiment 1 was that a fully–silvered mirror was used and thus participants could not see their hand during movement execution.

Results

MGA

A repeated–measures ANOVA applied on the non–perturbed trials showed that MGA increased for larger objects, $F(2,38) = 107.07, \epsilon = 0.61, p < .001$. The slope of the function relating MGA to object size was 0.46 ± 0.04 and therefore smaller than in Experiment 1. Figure 4.5 shows that, similar to Experiment 1, MGA was relatively well adapted to the new object size (second object size displayed) after an early perturbation whereas after a late perturbation MGA reflects the size of the object first displayed. We analyzed MGA using the same statistical procedures as in Experiment 1. When the MGA in the non–perturbed trials was compared to the MGA in the perturbed trials in which the object size actually grasped was the same there was a significant effect of perturbation type (early, late, none): LS–conditions: $F(2,38) = 28.18, \epsilon = 0.97, p < .001$, SL–conditions: $F(2,38) = 14.14, \epsilon = 0.98, p < .001$. Post-hoc tests confirmed that after an early perturbation MGA was of a similar size as in the no–perturbation conditions: The difference was $1.8mm \pm 0.9mm$ (p=.06) in the LS–conditions, and $1.1mm \pm 0.8mm$ (p=.18) in the SL–conditions. After a late perturbation MGA was $6.0mm \pm 0.8mm$ ($p < .001$) larger in the LS–conditions, and $4.2mm \pm 0.8mm$ ($p < .001$) smaller in the SL–conditions. The main effect of object size was significant in all conditions (all $p < .001$). No interactions were found (all $p > .10$).

The complementary analysis comparing the MGA in the non–perturbed trials with the MGA in the perturbed trials in which the object size displayed first was the same showed that in this case the MGA in the late perturbation trials did not differ from the MGA in the non–perturbed trials, $0.7mm \pm 0.6mm$ (p=.25) in the LS–conditions, and $1.1mm \pm 0.7mm$ (p=.16) in the SL–conditions. This finding indicates again that after a late perturbation the MGA reflects the size of the object first displayed. In summary the results are very similar to those of Experiment 1. The only difference was that MGA was overall larger when the hand was not visible

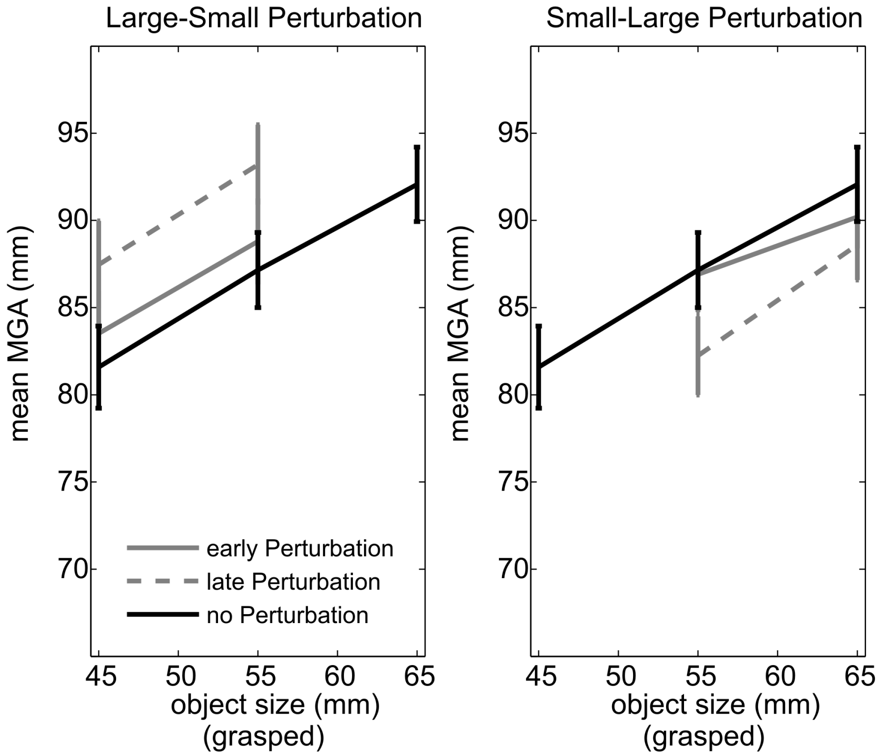


Figure 4.5: *Experiment 2: Maximum grip aperture as a function of grasped object size and perturbation time. The left panel shows the perturbation trials in which the object became 1 cm smaller and the right panel shows the perturbation in which the object became 1 cm larger. The black lines represent MGA in the non–perturbed trials. All error bars depict ± 1 SEM (between subjects). Note that participants were not able to see their hand during movement execution.*

during movement execution. This observation was statistically confirmed by an ANOVA with the within–subjects factor object size in the unperturbed trials and the between–subjects factor experiment, revealing a significant main effect of object size, $F(2, 76) = 357.48, \epsilon = 0.65, p < .001$, and the between–subjects factor experiment, $F(1, 38) = 19.04, p < .001$. The interaction was also significant, $F(2, 76) = 8.39, p = .003$.

Aperture profiles

Mean aperture profiles and the moment when the correction became visible during movement execution were calculated equivalently to Experiment 1. Figure 4.6 shows the mean aperture profiles and the corresponding correction times. Compared to Experiment 1 corrections occurred later. This holds for the early (LS–perturbation: 350 ms, SL–perturbation: 352 ms) as well as for the late perturbation condition (LS–perturbation: 287 ms, SL–perturbation: 246 ms). Again correction times were found to be shorter after a late perturbation than after an early perturbation.

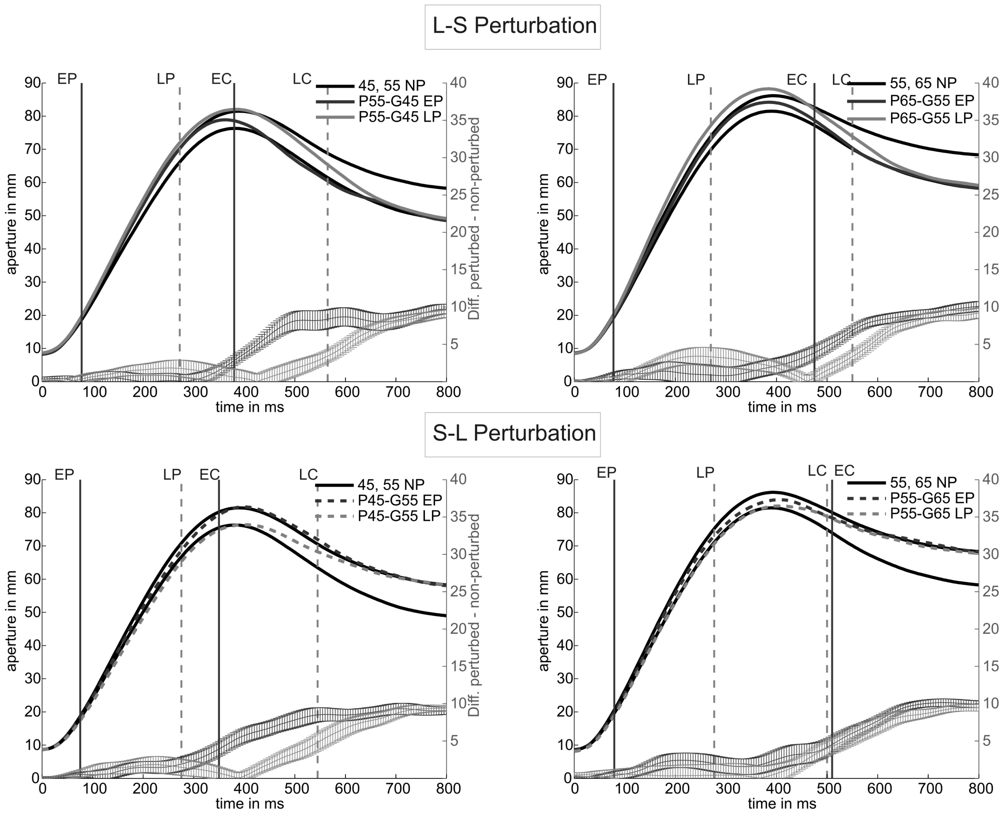


Figure 4.6: *Experiment 2: Mean aperture profiles for the different perturbation conditions when participants were not able to see their hand during movement execution. The solid black lines represent the aperture profiles in the non–perturbed trials. The vertical lines depict the perturbation and correction times in the different conditions (EP: early perturbation time, LP: late perturbation time, EC: early correction time, LC: late correction time). The lines with the error bars depict the mean differences between the perturbed and corresponding non–perturbed aperture profiles which were used to calculate correction times.*

Double–Peak Pattern

We determined the number of double–peaks in the different conditions as in Experiment 1. In contrast to Experiment 1 the repeated–measures ANOVA over all five conditions revealed an effect of condition, $F(4, 76) = 4.89, \epsilon = 0.62, p = 0.007$. Figure 4.4 shows that in the LS–perturbation conditions the percentage of double–peaks was slightly reduced whereas in SL–perturbation conditions there were slightly more double–peaks than in the no–perturbation condition. Post-hoc comparisons showed that compared to the no–perturbation condition only the difference to the late LS–perturbation condition became significant ($6.4\% \pm 2.3\%, p = 0.01$). As in Experiment 1 we found high correlation coefficients between the no–perturbation condition and the four different perturbation conditions (all $r > .81$) suggesting that double–peaks reflect an individual grasping pattern. As confirmed by an ANOVA with the between–subjects factor experiment the percentage of double–peaks was similar in Experiment 1 and 2, $F(1, 38) = 0.30, p = 0.59$. There was no significant interaction (p=.30).

Transport component

The transport component of the grasping movement was analyzed using the same dependent variables as in Experiment 1. No significant influences of perturbation condition (early, late, none) on the parameters MT, TPV, APV and TPD were found, neither in the LS–conditions nor in the SL–conditions (Table 2). Again wrist kinematics turned out to be very consistent over all conditions. The repeated–measures ANOVA with the between–subjects factor experiment revealed no differences in MT, TPV, APV and TPD between the experiments suggesting that wrist kinematics were uninfluenced by vision of the moving hand.

	MT	TPV	APV	TPD
non-perturbed (L)	667 (25)	220 (9)	0.96 (0.03)	371 (14)
LS early	663 (27)	222 (9)	0.96 (0.03)	366 (13)
LS late	683 (28)	220 (9)	0.97 (0.03)	363 (15)
non-perturbed (S)	670 (26)	219 (8)	0.95 (0.02)	370 (14)
SL early	678 (29)	217 (9)	0.96 (0.02)	364 (14)
SL late	678 (27)	219 (8)	0.95 (0.02)	372 (13)

Note. Standard errors are given in parentheses.

Table 2: Kinematic characteristics of the transport component during LS–perturbed and SL–perturbed trials (hand NOT visible during movement execution). MT: movement time (ms); TPV: time to peak velocity (ms); APV: amplitude of peak velocity (mm/ms); TPD: time to peak deceleration (ms).

Discussion

In this experiment we asked to what extent the corrective processes adjusting the grip after a size perturbation rely on visual feedback about the relative positions of hand and target. Therefore, we used exactly the same perturbation conditions as in Experiment 1 but prevented vision of the hand during grasping. So far, all studies applying the size–perturbation paradigm did not systematically investigate the role of the vision of the hand when grip adjustments were required. Most of these studies introduced size–perturbations by shifting the illumination from a small object to a large object to grasp and vice versa leaving the question open how well the hand was visible for the participants during the movement (e.g., Jeannerod, 1981; Paulignan, Jeannerod, et al., 1991; Castiello et al., 1993; Bennett & Castiello, 1995).

In accordance with studies investigating corrective processes in pointing movements we found that the correction characteristics of the grip were similar with and without vision of the moving hand (Prablanc & Martin, 1992; Komilis et al., 1993). For early perturbations participants were still able to adjust their grip to the new object size. This finding suggests that corrections are achieved in an open–loop way using continuous feed–forward mechanisms. According to the feed–forward models of motor control, error reductions are based on efference copies of the movement allowing the comparison between the current state and the planned future state of the effector (e.g. Wolpert, Ghahramani, & Jordan, 1995; Wolpert, Miall, & Kawato, 1998; Kawato, 1999). Possible discrepancies are accommodated by a change in the motor plan that is forwarded to the execution system reacting to this new information. The advantage of this kind of movement planning is that error can be corrected faster than in purely feedback based control systems in which the movement is planned by continuously comparing the relative locations of hand and target. Thus, visual information about the hand in relation to the object seems not to be mandatory to correct the motor output efficiently.

As many other studies suppressing vision of the moving hand we found that MGA was larger without vision of the hand (Wing et al., 1986; Jakobson & Goodale, 1991; Berthier et al., 1996; Churchill et al., 2000). Since the capability to adjust the grip on–line does not seem to depend on vision of the hand this finding suggests that such movements are programmed with a larger safety–margin in order to account for the higher uncertainty of the movement (c.f. Jakobson & Goodale, 1991).

Regarding the correction times of the movement we replicated the finding that corrections were initiated faster after late perturbations than after early perturbations. This supports the notion that corrections can be incorporated more easily in the end–phase of the grasp. However, according to Woodworth (1899) the adjustments in the end–phase of the movement are based on a direct comparison of the effector in relation to the target. Since our experiment clearly shows that vision of the hand relative to the target is not necessary to correct the movement other information sources than only visual ones are also used in this corrective end–phase.

So far our findings suggest that the availability of visual information about the hand influences grasping kinematics (e.g., larger MGA if the hand is not seen) but has only little effect on the corrections to the new object size. The adaptation to the new object size was mainly achieved by smooth changes in the aperture over time. These results indicate that small changes in object size are corrected by a smooth adjustment of the initially planned motor program using feed–forward mechanisms. However, it remains unclear whether small corrections are accomplished differently than larger adjustments. It might be that smaller corrections can be integrated smoothly in an ongoing movement whereas larger corrections require a reprogramming and substitution of the initially planned motor program (as indicated by a double–peak pattern). In Experiment 3 we tested for this possibility by introducing larger changes in object size (± 5/6 cm) occurring at the beginning of the movement.

4.4 Experiment 3

In this experiment we examined whether corrective processes of the grip are different when larger corrections are required (e.g., indication for the programming of a secondary sub–movement). Therefore, we introduced small (1 and 2 cm) and large (5 and 6 cm) changes in object size which occurred at movement onset.

Methods

Participants

Twenty undergraduate and graduate students of the University of Giessen (mean age = 25, SD = 6) participated in the experiment. They were paid 8 Euro per hour for participation. All participants were right-handed by self report and had normal or corrected-to-normal visual acuity. One experimental session lasted about 90 minutes.

Stimuli and Procedure

The apparatus was identical and the procedure very similar to Experiment 1. In order to vary the amplitude of the size perturbations we used other objects than in Experiment 1. The objects were 25, 35, 45 and 85 mm in length but had the same width (15 mm) and depth (15 mm) as in Experiment 1 and 2. By using a wider range of object sizes we were able to introduce small (1 and 2 cm) and large (5 and 6 cm) size perturbations (for a complete overview of all perturbation conditions see Table 3). In 75% of the trials no size–perturbation occurred (non–perturbed trials). In the remaining 25% of the trials the virtually presented object changed its size during the movement (perturbed trials). Each perturbation condition was presented six times and each non–perturbation condition was presented 36 times resulting in 192 trials. The perturbation occurred always at the beginning of the movement (corresponding to the early perturbation condition in Experiment 1 and 2). A half–transparent mirror was used such that participants could see their hand during movement execution.

		perturbation direction	
		large–small (LS)	small–large (SL)
perturbation size	small	P45-G25 P45-G35	P25-G45 P35-G45
	large	P85-G25 P85-G35	P25-G85 P35-G85

Table 3: Perturbation conditions of Experiment 3 (P indicates the size of the object size presented at the beginning of the movement, G indicates the size of the object grasped after the perturbation had occurred).

Results

MGA:

All analyses of the aperture were performed equivalent to Experiment 1 and 2. It should be noted that the large changes in object size, from 25 mm and 35 mm to 85 mm, posed a problem on the determination of MGA. When the object became larger it was often touched before MGA was actually reached meaning that MGA was determined at the moment of touch. This happened in $34.6\% \pm 5.6\%$ of the trials when grasping the 85 mm object in the non–perturbed condition; in $59.0\% \pm 7.1\%$ of the P25-G85 condition; and in $50.8\% \pm 5.6\%$ of the P35-G85 condition. In all other conditions, however, this was hardly ever observed ($0\% - 2.7\%$ of the trials).

Figure 4.7 depicts the MGA in the non–perturbed conditions and the corresponding perturbed conditions in which the object size grasped matched the size of the object not perturbed. Regarding the non–perturbed conditions (NP25, NP35, NP45, NP85) the MGA scaled to object size with a slope of 0.6 ± 0.03. Corrections were observed in all perturbation conditions and confirmed by statistical analyzes showing that all MGAs in the perturbation conditions were significantly different from the MGAs in the non–perturbed conditions when compared to the object size shown firstly (all $p < .001$). However, corrections were not accomplished perfectly in all conditions, particularly when the necessary adjustments became larger. In the small perturbation conditions (1 and 2 cm) only the P45-G25 differed significantly from grasping the 25 mm object in the non–perturbed condition. For larger changes of object size (5 and 6 cm) MGA always differed significantly from the MGA obtained in the non–perturbed trials (smaller in the SL and larger in the LS conditions, all $p < .001$). These findings suggest that the grip could not be adapted perfectly to the new object size until MGA was reached when larger corrections are required. Since movements for larger objects are initiated with a much higher acceleration of the fingers it is seems plausible that it also takes more time to decelerate and correct for the necessary changes.

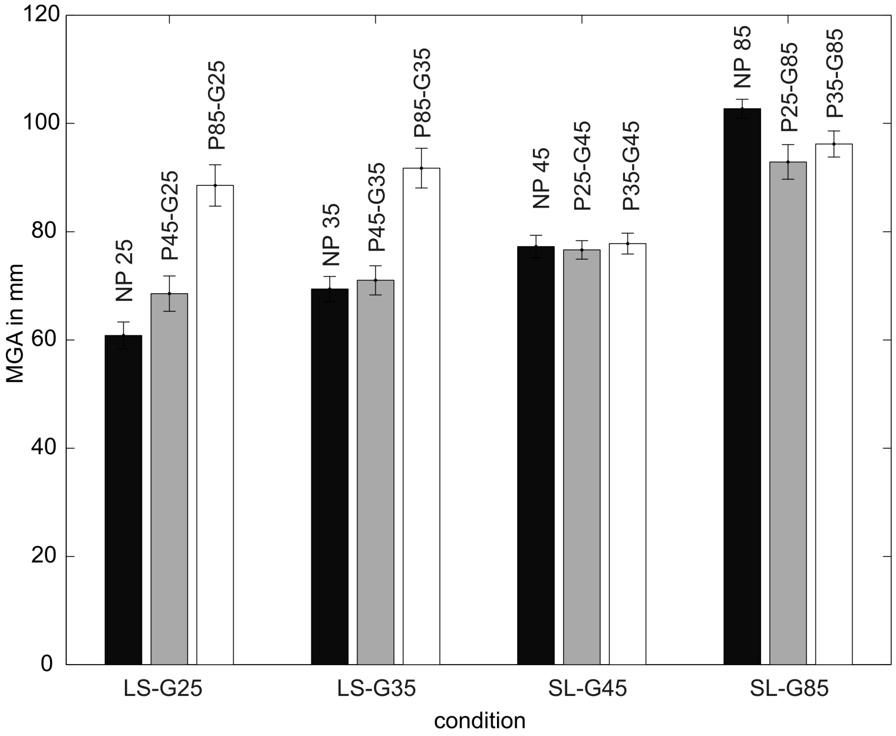


Figure 4.7: *Experiment 3: Maximum grip aperture in no–perturbation conditions compared to the MGA in the perturbation condition in which the same object size was grasped. All error bars depict ± 1 SEM (between subjects).*

Profiles:

Figure 4.8 shows the mean aperture profiles for all perturbed and non–perturbed conditions and the correction times respectively. Mean correction times were similar for the LS (264 ms) and the SL–condition (240 ms) when the change in object size was small (1 and 2 cm). These values are in a similar range as those obtained in Experiment 1. When the change in object size was large (5 and 6 cm) the correction time was shorter in SL–condition (195 ms) but not in the LS–condition (276 ms). The finding that corrections were observed earlier in MT when the object became much larger might indicate that adjustments can be accomplished faster if they are essentially necessitated. Moreover, this result is in accordance with the proposition of Glover et al. (2005) stating that SL–perturbations led to an earlier adjustment than LS–perturbations. In the study of Glover et al. (2005) also very large perturbations of object size were used ($\pm 5cm$).

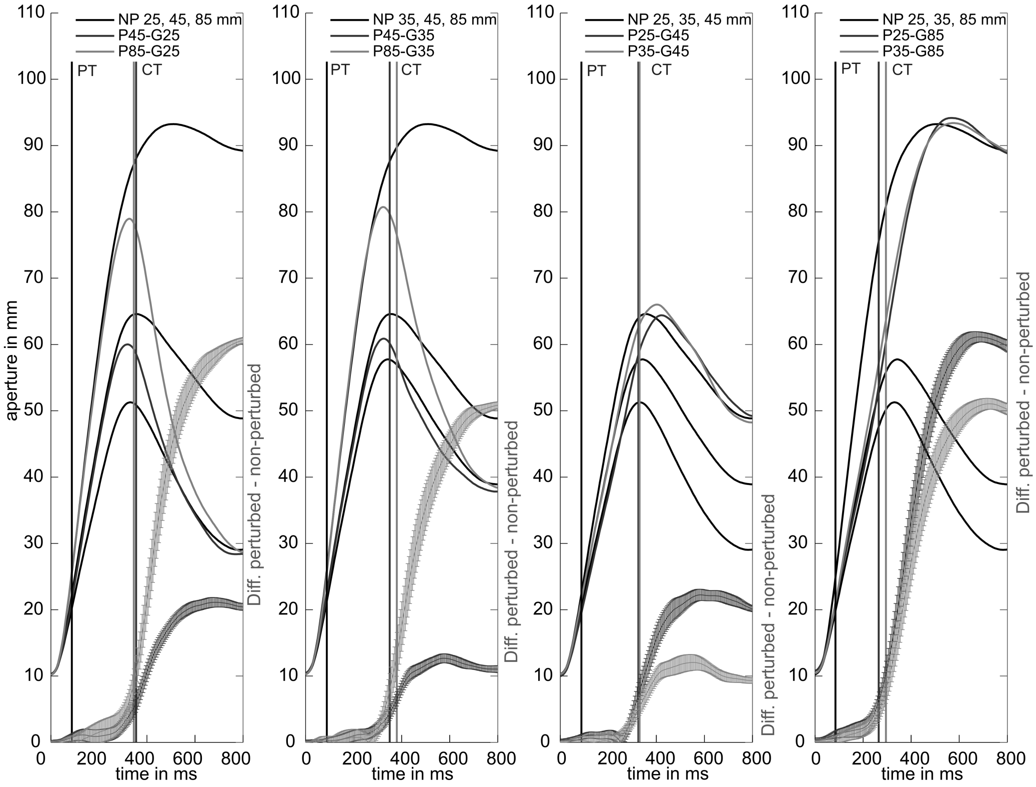


Figure 4.8: *Experiment 3: Mean aperture profiles for the different perturbation conditions. The solid black lines represent the aperture profiles in the relevant non–perturbed trials. The vertical lines depict the perturbation and correction times in the different conditions (PT: perturbation time, CT: correction time). The lines with the error bars depict the mean differences between the perturbed and corresponding non–perturbed aperture profiles which were used to calculate correction times.*

Double peak pattern:

The number of double–peaks observed was overall larger than in Experiment 1. The relation between the conditions, however, remained similar (Figure 4.9). There were slightly more double–peaks when the object became larger and slightly less double–peaks when the object became smaller. The repeated–measures ANOVA revealed a significant effect of condition, $F(4,76) = 5.0$, $\epsilon = 0.61$, $p = 0.007$. Post-hoc tests comparing the perturbation conditions with the no–perturbation condition showed that there were significant less double–peaks in the LS-large condition (8.8% ± 2.7%) and significant more double–peaks in the SL-small condition (5.4% ± 2.5%). One reason that we did not found more double–peaks in the SL–large condition might be that the object was often touched before MGA was reached (see above). However, double–peaks occurring after the touch of the object are performed on the basis of tactile feedback and are not any longer based on the visual information. Since we were interested in the corrective processes based on visual information peaks occurring after the touch of the object were not considered. Furthermore, we could replicate the finding that double–peaks occur more often in some participants than in others confirming the notion that double–peaks are an individual movement pattern (all $r > .89$).

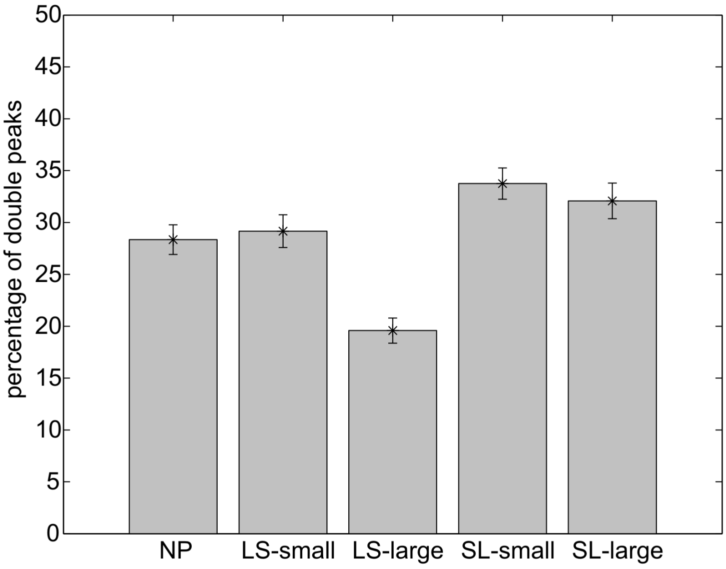


Figure 4.9: *Experiment 3: Mean percentage of double–peaks in the different conditions. All error bars depict ± 1 SEM (between subjects).*

Discussion

In this experiment we tested whether the corrective processes are different when the required adjustments of the grip are very large. Therefore, we introduced small and large changes of object size which occurred at the beginning of the movement. In contrast to Experiment 1 and 2 we found that MGA could not be adapted perfectly to the size of the new object when the applied perturbations were larger. This result confirms the expectation that the completion of larger corrections takes more time. Moreover, when the object became much larger the movement could often not be adjusted appropriately meaning that participants touched the object before MGA was reached. This finding might also be due to the fact that such extensive adaptations of the grip size represent a very unnatural situation. As shown by Castiello et al. (1993) large perturbations of object size would normally lead to a change in the grasp type used (from precision to power grip) rather than to an adjustment of the planned precision grip. The correction times for the perturbations were similar to those obtained in Experiment 1. Only in the condition in which the object became much larger corrections were found to start earlier (about 50 ms). This finding might indicate that when the adaption of the grip is absolutely essential for a successful movement corrections can be implemented faster.

In accordance with Experiment 1 and 2 we found again double–peaks in all conditions and a tendency to slightly more double–peaks in the grip pattern when object size increases and slightly less double–peaks when object size decreases. However, in about two thirds of the trials in which the object became larger no double–peaks were observed. During these movements corrections were accomplished by a smooth adjustment of the grip. This finding gives further evidence that double–peaks cannot be considered as a general movement strategy to correct for changes in object size. Paulignan, Jeannerod, et al. (1991) originally hypothesized that the double–peak pattern indicates the creation of a new movement plan which is superimposed on the old one. Based on our results we would argue that double–peaks represent regulatory processes of the movement which occur also in non–perturbed trials becoming more frequent when more corrections are required (e.g., when object size is perturbed).

4.5 General Discussion

We investigated the adaptability of the grip to changes in object size. We were especially interested in the characteristics of the corrective processes carried out by the motor system after a size perturbation. Up to now, it is a debate in the field of motor control whether movements are: (a) continuously regulated based on afferent information (and if so which kind of afferent information is used), (b) entirely planned in advance, or (c) a combination of pre–planned and current control processes (for review see Desmurget & Grafton, 2000). We addressed this issue by introducing perturbations of object size at two different moments in time (early/late) and varying whether participants were able to see their hand during movement execution (Experiment 1/Experiment 2).

In Experiment 1 we found that MGA was perfectly adapted to the new object size after an early perturbation, whereas this correction was not accomplished after a late perturbation. Movements in which the grip had to be adjusted in response to a size perturbation resembled movements in the non–perturbed conditions showing a single peak in the aperture profile in most trials. It was originally proposed that double–peaks in the grip profile represent a secondary sub–movement indicating that a new movement is programmed and superimposed on the old one (e.g., Paulignan, Jeannerod, et al., 1991). By looking for double–peaks in perturbed as well as non–perturbed trials we found that they occur almost equally often in all conditions (20% of the trials). Based on our results, we think that double–peaks can be regarded as corrective modifications of ongoing movements occuring also when the object size is not changed and becoming slightly more frequent when larger corrections (e.g., caused by a perturbation) are required. The appearance of such regulatory processes during non–perturbed movements was also reported by Heath, Hodges, Chua, and Elliott (1998) investigating the on–line control of pointing movements. Moreover, these findings argue against a pure pre–planning of the movement as proposed by Plamondon (1995b, 1995a). In fact, corrective modifications occurring during movement execution suggest that the movement is permanently monitored and can be adjusted if necessary.

In Experiment 2 we examined the relevance of visual information of the moving hand for grip adjustments. We found that correction characteristics after size perturbations were very similar with and without vision of the hand. As in Experiment 1, MGA was adapted to the new object size when the perturbation occurred at the beginning of the movement. The observation that the adjustments to the new object size are also achieved without vision of the hand is in accordance with forward models of motor control (e.g. Wolpert et al., 1995, 1998; Kawato, 1999). These models assume that the nervous system estimates the current and the future states of the motor apparatus combining sensory input and motor output. If any discrepancies are detected a corrective command will be generated to adjust the movement appropriately. Besides this similarity of the corrective processes we found a larger MGA when the hand could not be seen during the grasp. This finding indicates that such movements are programmed with a larger safety margin accounting for the increased uncertainty (cf. Jakobson & Goodale, 1991).

So far all studies using the size perturbation paradigm in grasping introduced the changes at the beginning of the movement and reported relatively long correction times of approximately 300 ms which are also comparable to our results (e.g., Paulignan, Jeannerod, et al., 1991; Castiello et al., 1993; Dubrowski et al., 2002; Bock & Jüngling, 1999). However, we found that after a late perturbation correction times were considerably shorter suggesting that modifications can be incorporated faster in the latter half of the movement. This finding is in line with the assumption that fast goal–directed movements consist of two phases: an initial phase which is primarily ballistic followed by a slower corrective phase used to adjust the movement (Woodworth, 1899). However, according to Woodworth (1899) movement adjustments performed in the second phase of the movement rely on feedback processes comparing the relative positions of hand and target. Since movement corrections were accomplished in a similar way without vision of the hand other feedback sources like proprioceptive feedback and/or efference copies also seem to be important during this control phase. The observation that corrections are mainly accomplished during the end–phase of the movement is also in accordance with the results of Heath et al. (1998). In this study it was shown that during pointing movements the visual information is monitored on–line and used to modify the latter half of the trajectory while the initial portion of the movement was strongly influenced by the properties of the object shown before the perturbation.

In Experiment 3 we showed that MGA could not be adapted perfectly to the new object size when the required movement corrections become very large. However, the corrections were accomplished in a qualitatively similar way indicating that the planned motor program was adjusted smoothly in most of the trials. In contrast to the Experiments 1 and 2 we found shorter correction times when the object became much larger at the beginning of the movement. This finding might indicate that adjustments which are essentially necessitated to execute a successful movement can be executed faster.

In summary our results support the notion that in response to size perturbations the motor program is modified centrally in an open–loop way. Thus, visual feedback about the moving hand is not necessary to correct the movement successfully. Another advantage of using feed–forward mechanisms is that errors in the movement trajectory can be corrected faster than in a feedback based control system. Concerning the time course of the adjustments, our findings suggest that corrections can be faster incorporated in the deceleration phase of the movement. Overall our experiments confirm that new visual information can easily be used to modify and adjust an ongoing movement and that this is done by using continuous feed–forward mechanisms.

So far there is only little knowledge of how the on–line control of grasping is realized by the brain and which areas might be involved. Using transcranial magnetic stimulation (TMS) Glover et al. (2005) showed that the parietal lobes contribute in the on–line monitoring and adjustment of actions. A recent study of Tunik et al. (2005) used TMS to generate virtual lesions in healthy human subjects in the anterior intraparietal sulcus (aIPS) which is assumed to play a crucial role in the control of grasping. Results showed that TMS to the aIPS delayed the adaptive response of the perturbed trials suggesting that aIPS is highly involved in the on–line control of the grasping movements. Based on these experiments the authors concluded that aIPS performs dynamic, goalbased, sensorimotor transformations involving ”at least three variables: the current sensory state (context), the currrent motor command and the current goal” (Tunik et al., 2007, p. T81). Thus, the aIPS might represent at least a part of the neural correlate of the feed–forward control system (e.g., Desmurget & Grafton, 2000; Wolpert et al., 1998).

Chapter 5

Conclusions and Outlook

In this thesis I examined the role of visual information for the planning, execution and control of grasping movements in three different studies. I was especially interested in the changes of grasping kinematics resulting from a change of the underlying visual information. Thus, grasping movements were not only investigated to gain insight in the processes of motor control but also to provide insight into the processes of perception. All experiments focused on the connection between perception and action in order to contribute to the understanding of the relationship of perceptual and motor processes. In the following I will shortly discuss the meaning of the obtained results in the light of the current knowledge about action and perception and their coupling.

5.1 Implications for the two visual system hypothesis

According to the model proposed by Milner and Goodale the output of the visual cortex is channeled into two anatomically distinct pathways: the dorsal cortical pathway assumed to generate automatic unconscious action and the ventral pathway assumed to generate conscious perception of the world. To recapitulate: Both pathways are assumed to fulfill different output requirements and are thus considered as two fundamentally different ways of dealing with the external world. Computations for the guidance of actions have to be fast. Since the position of an object can change quickly, the object representation is coded relative to the effector (egocentric frame of reference) and only stored for a very short time. In contrast, to identify and later recognize an object, the object representation has to be available over a long time meaning that a long term memory is needed. Moreover, the object should be coded relative to other objects and independent of the position of the effector (allocentric frame of reference). Consequently, the ventral and the dorsal pathway are assumed to create different output characteristics.

Since this hypothesis has become prominent many studies investigating grasping movements were inspired by perceptual questions testing for the predictions of the two visual system hypothesis. Very soon it has become a matter of debate whether the dissociation between perception and action is really as strict as originally proposed by Milner and Goodale. Up to now, many studies criticized one of the main predictions of the Milner and Goodale theory, which is the assumption that visually guided movements resist visual illusions while the conscious perception is deceived (e.g., Franz et al., 2000; Franz, 2001; Franz & Gegenfurtner, in press; Pavani et al., 1999; van Donkelaar, 1999; Smeets & Brenner, 1995; Smeets, Brenner, de Grave, & Cuijpers, 2002; Vishton, Pea, Cutting, & Nunez, 1999).

As already mentioned in the introduction, evidence for the different timing proposed for the dorsal and the ventral stream comes also mainly from illusion studies. In these studies it was argued that grasping movements executed under full vision or initiated when vision of the stimulus is available, are uninfluenced by the illusion (dorsal stream guidance) whereas introducing a delay leads to an illusion effect in grasping (ventral stream guidance). However, results were again ambiguous (e.g., Westwood et al., 2001; Heath et al., 2004, 2005). Moreover, we could recently show that there might be an alternative interpretation for the increased illusion effect in grasping after a delay (Franz et al., 2007). According to this study, the critical factor for the size of the illusion effect in grasping is the availability of visual feedback and not the existence of different memory systems in the dorsal and the ventral stream.

The advantage of using visual illusions as stimuli is that they introduce a dissociation between conscious perception of size, and the real metrics of the object which are assumed to be used to guide an action. Therefore, it is possible to test directly for the predictions of the two visual system hypothesis. The disadvantage, however, is that this procedure causes a lot of methodological problems making it difficult to compare the effects of the illusion in perceptual and action tasks (for review see Franz & Gegenfurtner, in press; Smeets, Brenner, de Grave, & Cuijpers, 2002). This long lasting debate suggests that measuring the effect of visual illusions on action and perception might be not the best way to find evidence for the two visual system hypothesis.

Before drawing conclusions from the examination of grasping movements using visual illusions the properties of grasping movements directed to "simple" stimuli should be known well. In the first study of this thesis I systematically investigated the effects of different delays on grasping kinematics when grasping simple objects (bars and discs). According to the real–time view of action which is a specification of the two visual system hypothesis, object visibility at the time of movement initiation is crucial for the kind of representation used (Westwood & Goodale, 2003; Westwood et al., 2003; Goodale et al., 2003, 2005). As long as the object is visible when the movement is initiated the movement is guided by the real–time computations of the dorsal stream. As soon as the object is not visible at movement initiation the stored ventral representation is used to guide the action resulting in changes of movement kinematics (e.g., larger MGA; Hu et al., 1999). Additionally to making very strong predictions the real–time hypothesis contradicts many of the earlier findings in grasping research. For example, it has been shown that preventing vision of the moving hand during movement execution results in changes of grasping kinematics (e.g., Wing et al., 1986; Jakobson & Goodale, 1991; Berthier et al., 1996). The results of the first study are in line with these earlier findings, and thus in contrast to the predictions of the real–time hypothesis. The main finding was that suppressing vision at the moment the movement was initiated already results in a large increase of MGA. Furthermore, we found that the increase in MGA due to longer delays can be very well described by an exponential function reflecting the information decay over time. Overall, no evidence was found that there are qualitative changes in movement kinematics indicating a transition from one representation to another (dorsal to ventral).

The second study presented in the thesis contradicts another strong prediction of the real–time view stating that visually guided movements are always calculated in real–time and cannot be influenced by any previous (visual) experience or any earlier movement programming. In contrast, our findings give evidence that the kinematics of visually guided movements are affected by the properties of a previously presented object.

In summary, it is relatively obvious that these results cannot refute the Milner and Goodale model since the dissociation between perception and action was never tested directly. Nevertheless, they put at least the strong version, the real–time view of action, into question providing counter evidence for two of the main predictions of this hypothesis. Besides, our experiments provide a large database showing how grasping kinematics are affected by: a) different delay conditions, b) different and basic object shapes (bars and disks), and c) physical changes of object size over a wide range of object sizes (1 - 10 cm). Thus, our data can be used as a baseline for the examination of more complex problems such as the effects of visual illusions.

Finally, the second study presented in this thesis suggests that perceptual and motor processes are closely linked. This finding seems not very surprising since perception and action almost never work in isolation when acting in every day life. Most of our activities like filling a glass of water, require the use of both modalities at the same time. Recent neuroimaging studies give also evidence that the cortical activation during perception and action tasks overlap largely (e.g., Faillenot et al., 1997, 1999). Since studies of normal brain functioning do not support the notion of a clear boundary between regions devoted to action and perception further work should concentrate more on the coupling of perception and action and on the question how both systems work together than on proving their, in some respects artificial, dissociation.

5.2 Implications for the control of grasping

In this thesis I focused on the investigation of the manipulation component of the grasping movement. In terms of the model proposed by Jeannerod (1981) the grasping movement consists of two relatively independent working components: the transport component carrying the hand to the object's location, and the manipulation component shaping the hand in anticipation of the grasp. According to this model the transport component is mainly influenced by the extrinsic properties of the object like its position, whereas the manipulation component depends on the intrinsic object properties like its size and shape. Since the initial proposition of that model many studies investigated the coupling of these components (e.g., Paulignan, MacKenzie, et al., 1991; Paulignan, Jeannerod, et al., 1991; Marteniuk et al., 1990; Bootsma & van Wieringen, 1992). Although our experiments were not primarily designed to study the relationship of transport and grasp component some of our findings are in line with the conception proposed by Jeannerod (1981). Firstly, we could show that MT which can be considered as a measure of the transport component was independent of the size of the object which is an intrinsic object property (cf. chapter 2.4). This finding holds over a very wide range of object sizes (1 - 10 cm) when the size of the contact surface of the object was kept constant. Secondly, in the size perturbation experiments (chapter 4) we found that other measures of the transport component were also uninfluenced by the size of the object as well as by the reorganization of the grip. The finding that changes in grip formation occur without affecting transport kinematics was one of the main arguments put forward in support of the independence of two visuomotor control systems (Jeannerod, 1981; Paulignan, Jeannerod, et al., 1991).

However, this very influential view of grasping was recently questioned by Smeets and Brenner (1999) proposing an alternative model which assumes that the final finger position is the controlled variable in prehension. The model, which predicts the movement of the fingers using the minimum jerk approach, results also in an apparent independence of grip and transport component without assuming the existence of two different visuomotor channels. Besides, the model of Smeets and Brenner (1999) provides also an alternative explanation to the proposed hierarchical relationship between the visuomotor channels (Paulignan, MacKenzie, et al., 1991; Paulignan, Jeannerod, et al., 1991). Basis of this hierarchy was the observation from perturbation studies showing that changes in object position result in an adjustment of the transport and the grasp component whereas changes in object size only affected the grasp component (which is also in accordance with the experimental results presented in chapter 4). Smeets, Brenner, and Biegstraaten (2002) were able to replicate this finding applying their model of independent digit control. Taken together, the model predicts most of the experimental results in grasping appropriately without sub–dividing grasping into two components (reviewed in Smeets & Brenner, 1999).

Regarding the experimental results obtained in this thesis most of them can be well fitted into the the grasping model of Smeets and Brenner (1999). That is, the independence of grip and transport component in the size perturbation study, the independence of the transport component from changes of object size, the influence of object size and reduced visual feedback on the timing of MGA, and the increase in MGA for: (a) larger object sizes, (b) reduced visual feedback, and (c) smaller contact surfaces of the target object. In terms of the Smeets and Brenner (1999) grasping model the increase in MGA in the latter two conditions is due to a more perpendicular approach to the objects surface (larger value of the approach parameter). One finding that is in conflict with the model is that we find an increase in MGA when visual information was reduced whereas we did not found the corresponding effect on the timing of MGA as predicted by the model (cf. Experiment 1 and 2 chapter 2, personal communication with Jeroen Smeets, December 20, 2007).

Outlook

Most of the results reported in this thesis fit well into both models being most prominent in the field of grasping at present. Unfortunately, on the basis of these findings we cannot decide which one is more appropriate to describe grasping movements formally. As shown in the previous paragraph, the model of Smeets and Brenner (1999) predicts relatively precisely the changes in grasping kinematics occurring in different conditions, such as changing the amount of visual feedback, or changing object size and object shape. However, neither the model of Smeets and Brenner (1999) nor the model of Jeannerod (1981) makes any suggestions how the opening and closing of the fingers during the movement might be controlled by the nervous system. Although some movement parameters vary with the task demands we could show that the grip pattern overall remains surprisingly stereotypical (see also Jeannerod, 1984). Based on this observation and the fact that little is known about which signals are sent by the CNS to the fingers to control their opening and closing we suggest a minimal model which might underly the observed regularity of the grip pattern (c.f. Ulrich & Wing, 1991).

According to this minimal model the aperture profile (distance between index finger and thumb) is assumed to consist of three phases: (I) acceleration phase, (II) phase of constant velocity, and (III) deceleration phase (figure 5.1). All phases are described mathematically using the formula of constant acceleration:

$$A = \frac{a}{2}t^2 + v_0 t + s_0$$

with: A: size of aperture; a: acceleration (constant); t: time; $v(0)$: initial velocity at $t = 0$; and $s(0)$: initial aperture at $t = 0$.

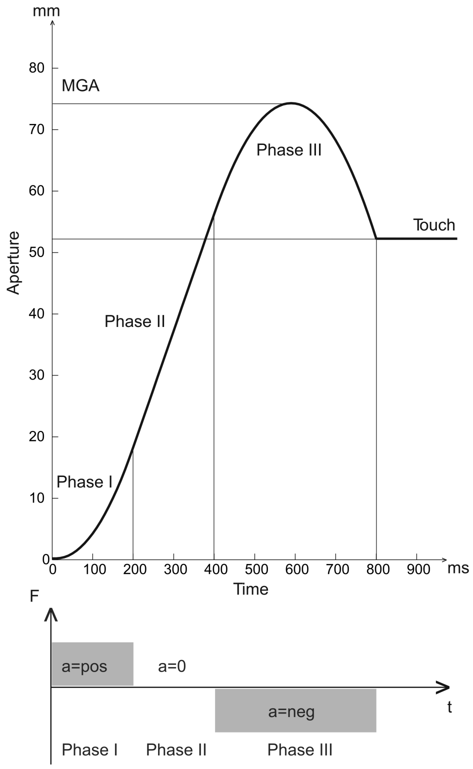


Figure 5.1: *Model description of the aperture profile when grasping with precision grip: Phase I: constant acceleration, Phase II: constant velocity and zero acceleration, Phase III: constant deceleration*

Thus, the fingers are considered as mass points to which a force is applied to open (accelerate) and to close (decelerate) them. These forces determine the strength and the duration of the phases and are expected to depend on the properties of the object to grasp (e.g., size) and on the requirements of the task (e.g., visual feedback). The advantage of the model is that the movement can be described by basic laws of physics specifying the signals which might be used by the CNS to control grasping.

A tentative application of the model on the datasets obtained in the first experimental series (chapter 2) revealed a satisfying fit when all four parameters of the model were freely chosen (strength of acceleration in the first phase, strength of deceleration in the third phase, and beginning and end of the second phase; Hesse & Franz, 2006). In a next step we aim at simplifying the model further by reducing the number of free parameters and revealing their dependence on different task demands. First attempts to explain the adaption of the grip by just varying one parameter e.g., higher acceleration in the first phase for larger objects, or prolongation of the second phase (linear phase) when visual feedback is reduced, showed that this might be possible (Hesse & Franz, 2006). However, testing the validity of the model and applying it to different datasets to test the appropriateness of the description is one of the challenges that will be addressed in future projects. Last but not least, the application of the model might also be interesting in the field of robotics specifying the signals which might be used to control the opening and closing of a robot hand.

References

Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size–contrast illusions deceive the eye but not the hand. *Current Biology*, *5*(6), 679–685.

Anderson, J. R., & Schooler, L. J. (1991). Reflections of the environment in memory. *Psychological Science*, *2*, 396–408.

Anderson, R. B., & Tweney, R. D. (1997). Artifactual power curves in forgetting. *Memory & Cognition*, *25*, 724–730.

Becker, W., & Fuchs, A. F. (1969). Further properties of the human saccadic system: eye movements and correction saccades with and without visual fixation points. *Vision Research*, *9*(10), 1247–1258.

Beggs, W. D., & Howarth, C. I. (1972). The accuracy of aiming at a target. Some further evidence for a theory of intermittent control. *Acta Psychologica*, *36*, 171–177.

Bennett, K. M., & Castiello, U. (1995). Reorganization of prehension components following perturbation of object size. *Psychology and Aging*, *10*(2), 204–214.

Berthier, N. E., Clifton, R. K., Gullapalli, V., McCall, D. D., & Robin, D. J. (1996).

Visual Information and Object Size in the Control of Reaching. *Journal of Motor Behavior*, *28*(3), 187–197.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., et al. (1998). Human anterior intraparietal area subserves prehension - a combined lesion and functional MRI activation study. *Neurology*, *50*(5), 1253–1259.

Binsted, G., Rolheiser, T. M., & Chua, R. (2006). Decay in visuomotor representations during manual aiming. *Journal of Motor Behavior*, *38*(2), 82–87.

Bock, O., & Jüngling, S. (1999). Reprogramming of grip aperture in a double-step virtual grasping paradigm. *Experimental Brain Research*, *125*(1), 61–66.

Bootsma, R. J., Marteniuk, R. G., MacKenzie, C. L., & Zaal, F. T. (1994). The speed-accuracy trade-off in manual prehension: effects of movement amplitude, object size and object width on kinematic characteristics. *Experimental Brain Research*, *98*(3), 535–541.

Bootsma, R. J., & van Wieringen, P. C. W. (1992). Spatio-temporal organisation of natural prehension. *Human Movement Science*, *11*(6), 205–215.

Bradshaw, M. F., & Watt, S. J. (2002). A dissociation of perception and action in normal human observers: the effect of temporal–delay. *Neuropsychologia*, *40*, 1766–1778.

Callaway, E. M. (2005). Structure and function of parallel pathways in the primate early visual system. *Journal Of Physiology-London*, *566*(1), 13–19.

Cant, J. S., Westwood, D. A., Valyear, K. F., & Goodale, M. A. (2005). No evidence for visuomotor priming in a visually guided action task. *Neuropsychologia*, *43*(2), 216–226.

Carey, D. P. (2001). Do action systems resist visual illusions? *Trends in Cognitive Sciences*, *5*(3), 109–113.

Carey, D. P., Harvey, M., & Milner, A. D. (1996). Visuomotor sensitivity for shape and orientation in a patient with visual form agnosia. *Neuropsychologia*, *34*(5), 329–337.

Carlton, L. (1981). Processing visual feedback information for movement control. *Journal of Experimental Psychology: Human Perception and Performance*, *7*(5), 1019–1030.

Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews Neuroscience*, *6*(10).

Castiello, U., Bennett, K., & Chambers, H. (1998). Reach to grasp: the response to a simultaneous perturbation of object position and size. *Experimental Brain Research*, *120*(1), 31–40.

Castiello, U., Bennett, K., & Stelmach, G. (1993). Reach to grasp: The natural response to perturbation of object size. *Experimental Brain Research*, *94*, 163–178.

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, *12*(4), 478–484.

Chua, R., & Elliott, D. (1993). Visual regulation of manual aiming. *Human Movement Science*, *12*, 365–401.

Churchill, A., Hopkins, B., Ronnqvist, L., & Vogt, S. (2000). Vision of the hand and environmental context in human prehension. *Experimental Brain Research*, *134*(1), 81–89.

Connolly, J. D., & Goodale, M. A. (1999). The role of visual feedback of hand position in the control of manual prehension. *Experimental Brain Research*, *125*(3), 281–286.

Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1998). Visuomotor priming. *Visual Cognition*, *5*(1–2), 109–125.

Craighero, L., Fadiga, L., Umilta, C. A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *Neuroreport*, *8*(1), 347–349.

Cuijpers, R. H., Smeets, J. B. J., & Brenner, E. (2004). On the relation between object shape and grasping kinematics. *Journal of Neurophysiology*, *91*, 2598–2606.

Dassonville, P., & Bala, J. K. (2004). Perception, action, and Roelofs effect: A mere illusion of dissociation. *Public Library of Science / Biology*, *2*(11), 1936–1945.

de Lussanet, M. H. E., Smeets, J. B. J., & Brenner, E. (2001). The effect of expectations on hitting moving targets: influence of the preceding target's speed. *Experimental Brain Research*, *137*(2), 246–248.

Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends In Cognitive Sciences*, *4*(11), 423–431.

DiPellegrino, J. W., Klatzky, R. L., & McCloskey, B. P. (1992). Time course of preshaping for functional responses to objects. *Journal of Motor Behavior*, *21*, 307–316.

Dubrowski, A., Bock, O., Carnahan, H., & Jüngling, S. (2002). The coordination of hand transport and grasp formation during single– and double–perturbed human prehension movements. *Experimental Brain Research*, *145*(3), 365–371.

Ebbinghaus, H. (1885). *Über das Gedächtnis. Untersuchungen zur experimentellen Psychologie.* Leipzig: Duncker & Humblot.

Faillenot, I., Decety, J., & Jeannerod, M. (1999). Human brain activity related to the perception of spatial features of objects. *Neuroimage*, *10*(2), 114–124.

Faillenot, I., Toni, I., Decety, J., Gregoire, M. C., & Jeannerod, M. (1997). Visual pathways for object-oriented action and object recognition: Functional anatomy with pet. *Cerebral Cortex*, *7*(1), 77–85.

Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences*, *5*(11), 457–459.

Franz, V. H. (2003). Manual size estimation: A neuropsychological measure of perception? *Experimental Brain Research*, *151*(4), 471–477.

Franz, V. H., & Gegenfurtner, K. R. (in press). Grasping visual illusions: Consistent data and no dissociation. *Journal of Cognitive Neuropsychology.*

Franz, V. H., Gegenfurtner, K. R., Bülthoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, *11*(1), 20–25.

Franz, V. H., Hesse, C., & Kollath, S. (2007). Grasping after a delay: More ventral than dorsal? *Journal of Vision*, *7*(9), 157a. (Poster presented at the Vision Sciences Society conference (VSS), Sarasota, Florida)

Franz, V. H., Scharnowski, F., & Gegenfurtner, K. R. (2005). Illusion effects on grasping are temporally constant, not dynamic. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(6), 1359–1378.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.

Garofeanu, C., Kroliczak, G., Goodale, M. A., & Humphrey, G. K. (2004). Naming and grasping common objects: a priming study. *Experimental Brain Research*, *159*(1), 55–64.

Gegenfurtner, K. R., & Hawken, M. J. (1996). Interaction of motion and color in the visual pathways. *Trends in Neurosciences*, *19*, 394–401.

Gentilucci, M., Chieffi, S., Daprati, E., Saetti, M. C., & Toni, I. (1996). Visual illusion and action. *Neuropsychologia*, *34*(5), 369–376.

Gentilucci, M., Chieffi, S., Scarpa, M., & Castiello, U. (1992). Temporal coupling between transport and grasp components during prehension movements: effects of visual perturbation. *Behavioural Brain Research*, *47*(1), 71–82.

Glover, S., Miall, R. C., & Rushworth, M. F. (2005). Parietal rTMS disrupts the initiation but not the execution of on-line adjustments to a perturbation of object size. *Journal of Cognitive Neuroscience*, *17*(1), 124–136.

Gnadt, J. W., Bracewell, R. M., & Andersen, R. A. (1991). Sensorimotor transformation during eye movements to remembered visual targets. *Vision Research*, *31*(4), 693–715.

Goodale, M. A., Cant, J. S., & Króliczak, G. (2006). Grasping the Past and Present: When Does Visuomotor Priming Occur? In H. Ögmen & B. G. Breitmeyer (Eds.), *The first half second - the microgenesis and temporal dynamics of unconsicious and conscious visual processes* (pp. 51–71). Cambridge, MA: MIT Press.

Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*, 1159–1178.

Goodale, M. A., Jakobson, L. S., Milner, D. I., A. D. ad Perrett, Benson, P. J., & Hietanen, J. K. (1994). The nature and limits of orientation and pattern processing supporting visuomotor control in a visual form agnosic. *Journal of Cognitive Neuroscience*, *6*, 46–56.

Goodale, M. A., Kroliczak, G., & Westwood, D. A. (2005). Dual routes to action: Contributions of the dorsal and ventral streams to adaptive behavior. *Progress in Brain Research*, *149*, 269–283.

Goodale, M. A., Meenan, J. P., Bülthoff, H. H., Nicolle, D. A., Murphy, K. J., & Carolynn, I. R. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, *4*(7), 604–610.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 97–112.

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*, 154–156.

Goodale, M. A., Pélisson, D., & Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature*, *320*, 748–750.

Goodale, M. A., Westwood, D. A., & Milner, A. D. (2003). Two distinct modes of control for object–directed action. *Progress in Brain Research*, *144*, 131–144.

Gordon, A. M., Forssberg, H., Johansson, R. S., & Westling, G. (1991). Visual size cues in the programming of manipulative forces during precision grip. *EBR*, *83*, 477–482.

Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *Neuroimage*, *6*(4), 231–236.

Greenhouse, S. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, *24*(2), 95–112.

Grèzes, J., & Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, *40*(2), 212–222.

Grèzes, J., Tucker, M., Armony, J., Ellis, R., & Passingham, R. E. (2003). Objects automatically potentiate action: an fMRI study of implicit processing. *European Journal of Neuroscience*, *17*(12), 2735–2740.

Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, *10*(1), 122–136.

Haffenden, A. M., & Goodale, M. A. (2000a). The effect of learned perceptual associations on visuomotor programming varies with kinematic demands. *Journal of Cognitive Neuroscience*, *12*(6), 950–964.

Haffenden, A. M., & Goodale, M. A. (2000b). Independent effects of pictorial displays on perception and action. *Vision Research*, *40*, 1597–1607.

Haffenden, A. M., & Goodale, M. A. (2002). Learned perceptual associations influence visuomotor programming under limited conditions: Kinematic consistency. *Experimental Brain Research*, *147*, 485–493.

Heath, M., Hodges, N. J., Chua, R., & Elliott, D. (1998). On-line control of rapid aiming movements: Unexpected target perturbations and movement kinematics. *Canadian Journal Of Experimental Psychology-Revue Canadienne De Psychologie Experimentale*, *52*(4), 163–173.

Heath, M., Rival, C., & Binsted, G. (2004). Can the motor system resolve a premovement bias in grip aperture? Online analysis of grasping the Müller-Lyer illusion. *Experimental Brain Research*, *158*(3), 378–384.

Heath, M., Rival, C., Westwood, D. A., & Neely, K. (2005). Time course analysis of closed– and open–loop grasping of the Müller-Lyer illusion. *Journal of Motor Behavior*, *37*(3), 179–185.

Held, R. (1970). Two modes of processing spatially distributed visual information. In F. O. Schmitt (Ed.), *The neurosciences second study program* (pp. 317–324). Cambridge, MA: MIT Press.

Hesse, C., & Franz, V. H. (2006). *Grasping: A stereotyped visuomotor pattern?* Poster presented at the European Conference on Visual Perception (ECVP), St Petersburg, Russia.

Hesse, C., & Franz, V. H. (submitted). Memory mechanisms in grasping.

Hoff, B., & Arbib, M. A. (1993). Models of trajectory formation and temporal interaction of reach and grasp. *Journal of Motor Behavior*, *25*, 175–192.

Hu, Y., Eagleson, R., & Goodale, M. A. (1999). The effects of delay on the kinematics of grasping. *Experimental Brain Research*, *126*, 109–116.

Hu, Y., & Goodale, M. A. (2000). Grasping after a delay shifts size–scaling from absolute to relative metrics. *Journal of Cognitive Neuroscience*, *12*(5), 856–868.

Hu, Y., Osu, R., Okada, M., Goodale, M. A., & Kawato, M. (2005). A model of the coupling between grip aperture and hand transport during human prehension. *Experimental Brain Research*, *167*(2), 301–304.

Jakobson, L. S., Archibald, Y. M., Carey, D. P., & Goodale, M. A. (1991). A kinematic analysis of reaching and grasping movements in a patient recovering from optic ataxia. *Neuropsychologia*, *29*, 803–809.

Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher–order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research*, *86*, 199–208.

Jax, S. A., & Rosenbaum, D. A. (2007). Hand path priming in manual obstacle avoidance: Evidence that the dorsal stream does not only control visually guided actions in real time. *Journal Of Experimental Psychology-Human Perception And Performance*, *33*(2), 425–441.

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In J. Long & A. Baddeley (Eds.), *Attention and performance* (Vol. 9, pp. 153–168). Hillsdale, NJ: Erlbaum.

Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, *16*(3), 235–254.

Jeannerod, M. (1999). Visuomotor channels: Their integration in goal-directed prehension. *Human Movement Science*, *18*(2–3), 201–218.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends in Neurosciences*, *18*, 314–320.

Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia*, *32*(4), 369–380.

Jennings, J. R. (1987). Editorial policy on analyses of variance with repeated measures. *Psychophysiology*, *24*(4), 474–478.

Johansson, R. S., & Westling, G. (1988). Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *EBR*, *71*, 59–71.

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion In Neurobiology*, *9*(6), 718–727.

Keele, S. W., & Posner, M. (1968). Processing of visual feedback in rapid movements. *Journal of Experimental Psychology*, *77*, 155–158.

Komilis, E., Pélisson, D., & Prablanc, C. (1993). Error processing in pointing at randomly feedback–induced double–step stimuli. *Journal of Motor Behavior*, *25*(4), 299–308.

Lawrence, D. G., & Hopkins, D. A. (1976). The development of motor control in the rhesus monkey: evidence concerning the role of corticomotoneuronal connections. *Brain*, *99*, 235–254.

Lawrence, D. G., & Kuypers, H. G. (1968a). The functional organization of the motor system in the monkey. II. The effects of lesions of the descending brain–stem pathways. *Brain*, *91*, 15–36.

Lawrence, D. G., & Kuypers, H. G. (1968b). The functional organization of the motor system in the monkey. I. The effects of lesions of bilateral pyramidal lesions. *Brain*, *91*, 1–14.

Livingstone, M. S., & Hubel, D. H. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, *240*, 740–749.

Loftus, G. R., Duncan, J., & Gehrig, P. (1992). On the time course of perceptual information that results from a brief visual presentation. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(2), 530–549.

Marteniuk, R. G., Leavitt, J. L., MacKenzie, C. L., & Athenes, S. (1990). Functional relationships between grasp and transport component in a prehension task. *Human Movement Science*, *9*, 149–176.

Maxwell, S. E. (2004). The persistence of underpowered studies in psychological research: Causes, consequences, and remedies. *Psychological Methods*, *9*(2), 147–163.

Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.

Meulenbroek, R. G., Rosenbaum, D. A., Jansen, C., Vaughan, J., & Vogt, S. (2001). Multijoint grasping movements. Simulated and observed effects of object location, object size, and initial aperture. *Experimental Brain Research*, *138*(2), 219–234.

Milgram, P. (1987). A spectacle–mounted liquid–crystal tachistoscope. *Behavior Research Methods, Instruments, & Computers*, *19*(5), 449–456.

Milner, A. D., Dijkerman, H. C., Pisella, L., McIntosh, R. D., Tilikete, C., Vighetto, A., et al. (2001). Grasping the past. delay can improve visuomotor performance. *Current Biology*, *11*(23), 1896–1901.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action.* Oxford: Oxford University Press.

Milner, A. D., Perrett, D., Johnston, R., Benson, P., Jordan, T. R., Heeley, D. W., et al. (1991). Perception and action in "visual form agnosia". *Brain*, *114*, 405–428.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, *6*, 414–417.

Mon-Williams, M., & Tresilian, J. R. (2001). A simple rule of thumb for elegant prehension. *Current Biology*, *11*, 1058–1061.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area aip. *Journal Of Neurophysiology*, *83*(5), 2580–2601.

Murphy, K. J., Racicot, C. I., & Goodale, M. A. (1996). The use of visuomotor cues as a strategy for making perceptual judgments in a patient with visual form agnosia. *Neuropsychology*, *10*(3), 396–401.

Nakayama, K., Song, J.-H., Finkbeiner, M., & Caramazza, A. (2007). Hand trajectories reveal cognitive states. *Journal of Vision*, *7*(9), 568-568.

Napier, J. R. (1956). The prehensile movements of the human hand. *Journal of Bone and Joint Surgery*, *38*, 902–913.

Paulignan, Y., Jeannerod, M., MacKenzie, C., & Marteniuk, R. (1991). Selective perturbation of visual input during prehension movements: 2. The effects of changing object size. *Experimental Brain Research*, *87*, 407–420.

Paulignan, Y., MacKenzie, C., Marteniuk, R., & Jeannerod, M. (1991). Selective perturbation of visual input during prehension movements: 1. The effects of changing object position. *Experimental Brain Research*, *83*, 502–512.

Pavani, F., Boscagli, I., Benvenuti, F., Rabuffetti, M., & Farnè, A. (1999). Are perception and action affected differently by the Titchener circles illusion? *Experimental Brain Research*, *127*, 95–101.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain*, *111*, 643–674.

Plamondon, R. (1995a). A kinematic theory of rapid human movements. Part II: Movement time and control. *Biological Cybernetics*, *72*(4), 309–320.

Plamondon, R. (1995b). A kinematic theory of rapid human movements. Part I: Movement representation and generation. *Biological Cybernetics*, *72*(4), 295–307.

Prablanc, C., & Martin, O. (1992). Automatic control during hand reaching at undetected two–dimensional target displacements. *Journal of Neurophysiology*, *67*(2), 455–469.

Prablanc, C., Pélisson, D., & Goodale, M. A. (1986). Visual control of reaching movements without vision of the limb. *Experimental Brain Research*, *62*, 293–302.

Rizzolatti, G., Carmarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. ii. area f5 and the control of distal movements. *Experimental Brain Research*, *71*(3), 491–507.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*(2), 131–141.

Rolheiser, T. M., Binsted, G., & Brownell, K. J. (2006). Visuomotor representation decay: influence on motor systems. *Experimental Brain Research*, *173*(4), 698–707.

Rosenbaum, D. A. (1991). *Human Motor Control*. Academic Press.

Rosenbaum, D. A., Meulenbroek, R. J., Vaughan, J., & Jansen, C. (2001). Posture-based motion planning: applications to grasping. *Psychological Review*, *108*(4), 709–734.

Rossetti, Y. (1998). Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Consciousness and Cognition*, *7*(3), 520–558.

Rossetti, Y., Pisella, L., & Vighetto, A. (2003). Optic ataxia revisited: Visually guided action versus immediate visuomotor control. *Experimental Brain Research*, *153*(2), 171–179.

Roy, A. C., Paulignan, Y., Meunier, M., & Boussaoud, D. (2006). Prehension movements in the macaque monkey: effects of perturbation of object size and location. *Experimental Brain Research*, *169*(2), 182–193.

Santello, M., Flanders, M., & Soechting, J. F. (2002). Patterns of hand motion during grasping and the influence of sensory guidance. *Journal of Neuroscience*, *22*(4), 1426–1435.

Saunders, J., & Knill, D. (2003). Humans use continuous visual feedback from the hand to control reaching movements. *Experimental Brain Research*, *152*(3), 341–352.

Savelsbergh, G. J. P., Steenbergen, B., & vanderKamp, J. (1996). The role of fragility information in the guidance of the precision grip. *Human Movement Science*, *15*(1), 115–127.

Schenk, T. (2006). An allocentric rather than perceptual deficit in patient DF. *Nature Neuroscience*, *9*, 1369–1370.

Schettino, L. F., Adamovich, S. V., & Poizner, H. (2003). Effects of object shape and visual feedback on hand configuration during grasping. *Experimental Brain Research*, *151*(2), 158–166.

Schiller, P. H., & Logothetis, N. K. (1990). The color–opponent and broad–band channels of the primate visual system. *Trends in Neurosciences*, *13*, 392–398.

Schneider, G. E. (1969). Two visual systems: Brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions. *Science*, *163*, 895–902.

Smeets, J. B. J., & Brenner, E. (1995). Perception and action are based on the same visual information: Distinction between position and velocity. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 19–31.

Smeets, J. B. J., & Brenner, E. (1999). A new view on grasping. *Motor Control*, *3*, 237–271.

Smeets, J. B. J., & Brenner, E. (2006). 10 years of illusions. *Journal of Experimental Psychology — Human Perception and Performance*, *32*, 1501–1504.

Smeets, J. B. J., Brenner, E., & Biegstraaten, M. (2002). Independent control of the digits predicts an apparent hierarchy of visuomotor channels in grasping. *Experimental Brain Research*, *136*, 427–432.

Smeets, J. B. J., Brenner, E., de Grave, D. D. J., & Cuijpers, R. H. (2002). Illusions in action: Consequences of inconsistent processing of spatial attributes. *Experimental Brain Research*, *147*, 135–144.

Trevarthen, C. B. (1968). Two mechanisms of vision in primates. *Psychologische Forschung*, *31*, 299–337.

Tunik, E., Frey, S. H., & Grafton, S. T. (2005). Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nature Neuroscience*, *8*(4), 505–511.

Tunik, E., Rice, N. J., Hamilton, A., & Grafton, S. T. (2007). Beyond grasping: Representation of action in human anterior intraparietal sulcus. *Neuroimage*, *36*, 77–86.

Ulrich, R., & Wing, A. M. (1991). A recruitment theory of force-time relations in the production of brief force pulses: The parallel force unit model. *Psychological Review*, *98*(2), 268–294.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

van Donkelaar, P. (1999). Pointing movements are affected by size–contrast illusions. *Experimental Brain Research*, *125*, 517–520.

van Sonderen, J. F., & van der Gon, J. J. D. (1991). Reaction–time–dependent differences in the initial movement direction of fast goal–directed arm movements. *Human Movement Science*, *10*, 713–726.

Vasey, M. W., & Thayer, J. F. (1987). The continuing problem of false positives in repeated measures ANOVA in psychophysiology: A multivariate solution. *Psychophysiology*, *24*(4), 479–486.

Vishton, P. M., Pea, J. G., Cutting, J. E., & Nunez, L. N. (1999). Comparing effects of the horizontal–vertical illusion on grip scaling and judgment: Relative versus absolute, not perception versus action. *Journal of Experimental Psychology — Human Perception and Performance*, *25*, 1659–1672.

Weir, P. L., MacKenzie, C. L., Marteniuk, R. G., & Cargoe, S. L. (1991). Is object texture a constraint on human prehension: kinematic evidence. *Journal of Motor Behavior*, *23*, 205–210.

Weir, P. L., MacKenzie, C. L., Marteniuk, R. G., Cargoe, S. L., & Fraser, M. B. (1991). The effects of object weight on the kinematics of prehension. *Journal of Motor Behavior*, *23*, 192–204.

Westwood, D. A., Chapman, C. D., & Roy, E. A. (2000, February). Pantomimed actions may be controlled by the ventral visual stream. *Experimental Brain Research*, *130*(4), 545–548.

Westwood, D. A., & Goodale, M. A. (2003). Perceptual illusion and the real–time control of action. *Spatial Vision*, *16*(3–4), 243–254.

Westwood, D. A., Heath, M., & Roy, E. A. (2000, October). The effect of a pictorial illusion on closed-loop and open-loop prehension. *Experimental Brain Research*, *134*(4), 456–463.

Westwood, D. A., Heath, M., & Roy, E. A. (2003). No evidence for accurate visuomotor memory: systematic and variable error in memory-guided reaching. *Journal of Motor Behavior*, *35*(2), 127–133.

Westwood, D. A., McEachern, T., & Roy, E. A. (2001). Delayed grasping of a Müller–Lyer figure. *Experimental Brain Research*, *141*, 166–173.

Wickelgren, W. A. (1970). Time, interference, and rate of presentation in short-term recognition memory for items. *Journal of Mathematical Psychology*, *7*, 219–235.

Wing, A. M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. *Journal of Motor Behavior*, *18*, 245–260.

Winges, S. A., Weber, D. J., & Santello, M. (2003). The role of vision on hand preshaping during reach to grasp. *Experimental Brain Research*, *152*(4), 489–498.

Wixted, J. T., & Ebbesen, E. B. (1997). Genuine power curves in forgetting: A quantitative analysis of individual subject forgetting functions. *Memory & Cognition*, *25*, 731–739.

Wolpert, D. M., Ghahramani, Z., & Jordan, M. (1995). An internal model for sensorimotor integration. *Science*, *269*, 1880–1882.

Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends In Cognitive Sciences*, *2*(9), 338–347.

Woodworth, R. (1899). The accuracy of voluntary movement. *Psychological Review Monograph*, *3*(2), 1–114.

Zaal, F. T. J. M., & Bootsma, R. J. (1993). Accuracy demands in natural prehension. *Human Movement Science*, *12*, 339–345.

Danksagung

An der Entstehung dieser Arbeit waren einige Menschen beteiligt, bei denen ich mich herzlich bedanken möchte. Insbesondere gilt mein Dank meinem Doktorvater Dr. Volker Franz für die wertvolle fachliche Betreuung bei der Anfertigung dieser Dissertation. Desweiteren danke ich Herrn Prof. Karl Gegenfurtner als Leiter der Abteilung sowie allen übrigen Mitarbeiterinnen und Mitarbeitern für ihre fortwährende Unterstützung. Mein Dank richtet sich auch an Jeroen Smeets und Eli Brenner, welche mir einen Forschungsaufenthalt an der Universität Amsterdam ermöglichten und damit den Grundstein für das Entstehen eines übernationalen Projekts legten. Dank je wel!

Im Speziellen danke ich Denise de Grave, die mir jederzeit mit Rat und Tat zur Seite stand, sich für fachliche Diskussionen Zeit nahm und mir hilfreiche Anregungen und Hinweise gab, die zum Gelingen dieser Arbeit beitrugen. Ebenso herzlich danke ich Jan Drewes für seine unkomplizierte Hilfe bei computertechnischen Problemen aller Art, sowie Martin Stritzke und Kai Hamburger für ihre Geduld beim Korrekturlesen meiner Texte.

Neben diesen fachlichen Hilfen gilt mein inniger Dank all jenen Menschen, die mir die drei Jahre in Gießen zu einer unvergesslichen Zeit haben werden lassen: Meiner Mitbewohnerin Johanna für die endlosen WG–Abende und fachlichen wie nicht fachlichen Diskussionen bei unzähligen Wein- und Whiskeyflaschen. Jutta und Martin, die mir zu lieben Freunden geworden sind und stets dafür gesorgt haben, dass es bei und neben der Arbeit genug zu lachen gab. Sie alle kennen die Höhen und Tiefen um das Entstehen dieser Arbeit und gaben mir den notwendigen persönlichen und moralischen Rückhalt.

Gießen, 21. Januar 2008

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, 20.Januar 2008 Constanze Hesse