SEVENTH FRAMEWORK
PROGRAMME

Project Acronym:	GRASP
Project Type:	IP
Project Title:	Emergence of Cognitive Grasping through Introspection, Emulation and Surprise
Contract Number:	215821
Starting Date:	01-03-2008
Ending Date:	28-02-2012

GRASP
Emergence of Cognitive Grasping through
Introspection, Emulation and Surprise

Deliverable Number:	D2
Deliverable Title :	Acton related attention in grasping
Type:	PU
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Contractual Date of Delivery to the EC:	28-02-2009
Actual Date of Delivery to the EC:	28-02-2009

Contents

4. Attached publications

Attachment 1: Hesse, C. & Deubel, H. (Human Movement Science, in press). Changes in grasping kinematics due to different start postures of the hand.

Chapter 1

Executive summary

This deliverable is part of WP1 – "Learning to Observe Human Grasping and Consequences of Grasping". The main part of the deliverable (Chapter 2) summarises and discusses the current state-of-the-art of the research in cognitive psychology and neuroscience on the role of selective, attentional processing in human reaching and grasping, with an emphasis on the behavioural studies in human prehension. Attention is of particular importance for the control of goal-directed behaviour, since recent research in primate action preparation and control has shown that there exists an intimate relationship between selective visual processing and the preparation and control of action. Indeed, one of the most striking features of the behaviour of higher mammals is its selectivity. "Selection-for-action" ensures that particular actions to particular goals are selected, while many other potentially possible actions that are automatically evoked by the visual inputs are not released. Think of an apparently trivial task where the actor has to pick up a specific glass from a table holding several other glasses. Obviously, very elaborate mechanisms had to evolve to select efficiently among these competing stimuli. These selection mechanisms have been associated with the phenomenon of attention, in which the mind selects one input for processing from a multitude of sensory inputs, at the expense of other perceptual inputs.

The findings summarized in the chapter provide important and novel implications for the development of artificial, robot systems that grasp like humans. They form the basis for initial conceptual models of *what* the grasp-relevant information is that is extracted in a particular task from the visual input and *how* this information is extracted. The output of this work within WP1 is provided to WP2 where it is required to understand and interpret human activities in order to map them into robotic embodiments.

Chapter 3 describes our recent investigations which studied in a series of experiments the coupling of transport, manipulation, and orientation components of human hand movements when grasping cylindrical objects. As one of the hallmarks of the classical studies on grasping, hand transport and hand shaping were identified as the two basic components of human grasping movements. These components are normally found to be well coordinated so that objects of varying size and shape resting in diverse locations can be grasped effectively. However, it is still a matter of debate how independent of each other these components really are. Obviously, this is an important question since the different views on their dependence and coordination imply fundamentally different explanations of the primate control of grasping, which are in turn of fundamental relevance for the task to implement a grasp controller. To study the coupling of these components, an experimental paradigm has been developed which analysed the effects of various starting postures on the kinematics of the human grasp. Quite strikingly, we find that grasping kinematics change considerably if the start posture of the hand is varied, arguing against a fixed coupling between the components. The complete publication (Human Movement Science, in press) can be found in Attachment 1.

Chapter 2

Attention in reaching and grasping

2.1 Introduction

The most fundamental function of vision is to guide motor output. All animals that have a good sense of vision use it to prepare their movements. The brain as a whole has therefore often been characterized as a sensory-motor interface that selects visuo-spatial information about the environment and transforms it into goal-directed movements. This is certainly true for the large portion of cortical areas in primates that are involved in visual sensation and/or action planning, like the fronto-parietal network and occipital cortex. Also, it has soon become evident that perception and action are functionally tightly intermingled and interactive. Together they form a repetitive 'perceive-to-action' cycle, which has its neural basis in a reciprocally interconnected network of visual and motor-related brain structures.

Also humans produce a wide variety of movement patterns, and among these the motor functions of the hands are exceptionally dexterous. When carefully observing how humans manually act on objects it becomes apparent that vision provides the most important source of the information that is needed to successfully interact with objects surrounding us. Here we review recent studies on the selective processing of visual input that is required for the preparation and control of manual reaching and grasping movements. A specific focus of the review will be on the preparation of those types of goal-directed movements in which two or more spatially separate, action-relevant locations have to be considered in the movement planning, such as in movements around an obstacle, in movement sequences, and in grasping. The reviewed experiments will reveal a close relationship between movement preparation and the deployment of visual attention, demonstrating the importance of what we term "visual preparation", i.e. the spatially selective, action-specific extraction of motor-relevant information from the visual scene.

2.2 Visual attention and the control of action

Most of the early investigations on visual attention related to purely perceptual tasks. Traditionally, the major aspects of studies on visual attention were to investigate how attention facilitates the detection of visual objects (e.g., Posner, 1980), their identification (e.g., Treisman, 1988; Desimone & Duncan, 1995), or their entry in the short-term memory (Duncan & Humphreys, 1989). From a functional point of view, Allport (1980, 1987) and Neumann (1987) were among the first to add a new perspective by pointing out that also spatio-motor actions imply selection processes. In natural, complex environments, goal-directed actions — such as grasping for a certain object in a cluttered scene — involve selective mechanisms that select the motor goal and extract the relevant visual parameters (e.g., the object's position in space as well as its orientation and size). These parameters must be extracted for the specific movement goal only, while excluding any effects of action-irrelevant distracters such as other objects in the scene. This selective processing has been referred to as 'parameter specification' (Neumann, 1987) or 'selection-for-action' (Allport, 1987). Milner and Goodale (1995) later modified the well-known distinction of the two visual processing streams along the ventral and dorsal pathway (see Mishkin et al., 1983) and emphasized the importance of the dorsal route for the computation of *action-related*, spatial information. Jeannerod's (1994) terminology of 'pragmatic mode' computations along the dorsal stream had a similar tenor.

To date there is a good amount of evidence linking selective attention and *oculomotor* planning. Rizzolatti and colleagues for example examined the effects of covert attention shifts on saccade trajectories when subjects were instructed to perform saccades either into the right or the left hemifield (Rizzolatti et al., 1987). Saccade trajectories systematically deviated according to the covertly attended location, i.e., the covert allocation of attention perturbed the ongoing oculomotor programming. More recently, Sheliga and colleagues (Sheliga, Riggio, Craighero, Rizzolatti, 1995) and Van der Stigchel & Theeuwes (2005) described similar results. Based on their findings Rizzolatti and colleagues (1987) formulated the *premotor theory of attention* which stated that covert shifts of attention precede saccadic motor output and that attention and saccadic programming share common neural structures. Several other studies also found a close link between the programming of eye movements and visual attention. Hoffman and Subramaniam (1995) had their participants saccade to an instructed location and also to detect a visual target presented just before the eye movement. By systematically varying the relative location of the discrimination target they analyzed the spatial deployment of attention during the phase of motor programming. The main result was that target discrimination was superior at locations to which a saccade was currently programmed. Similarly, Deubel and Schneider (1996) found increased discrimination performance in a letter discrimination task if the saccade goal spatially coincided with the location of the discrimination letter (see also Schneider & Deubel, 2002, and Baldauf & Deubel, 2008). Electrophysiological studies also documented shifts of covert attention during saccade preparation resulting in benefits in visual processing at the intended goal-location (Wauschkuhn et al., 1998; Eimer et al., 2006, 2007; Van der Stighel, 2006). More recently, a couple of behavioural studies further investigated the exact temporal dynamics of the described presaccadic attention shifts (Deubel, 2008; Castet et al., 2006). Concordantly, they found perceptual facilitation at the goal location to rise as early as 100ms after movement cue presentation, well before saccade onset. These results precisely document the weighting effects of oculomotor preparation on visual perception and how a saccade plan triggers covert shifts of attention to the intended location in order to select spatial parameters that are needed to produce the appropriate motor responses. Given the tight coupling of visual attention and oculomotor control it has become an important research topic to investigate whether both functions also share a common neural substrate (Nobre et al., 2000; Perry & Zeki, 2000). It is now widely accepted that cortical structures that are activated before oculomotor responses are also functionally involved in covert shifts of attention (for reviews see Corbetta, 1998; Moore et al., 2003, and Awh et al., 2006).

2.3 Attentional selection of an intended manual reach goal

The primate eye movement system is certainly one of the best-studied motor systems. We may ask whether the oculomotor system is so tightly coupled to visual attention because of its special role, namely that the rotation of the eye-ball immediately changes the input of the visual system. On the other hand, also the motor responses with other effectors may need to be planned on the basis of visual information although here it seems less obvious why the preparation of hand movements should influence perception as well. Actually, the premotor theory of visual attention (Rizzolatti et al., 1994, see also Rizzolatti, 1983; Rizzolatti & Camarda, 1987) is not explicitly restricted to the attentional preparation of oculomotor responses, but implicates a more general relation between visual attention and any kind of motor preparation. Apart from saccadic eye movements, every goal-directed spatiomotor action, most prominently hand movements, should focus visual processing onto the movement goal.

Indeed, a number of recent experimental studies have emphasized the fact that also the preparation manual responses employ the allocation of attention to the intended movement goal. Some of these studies use overt attention, i.e. the eye-fixation behaviour, as an indicator of attention. So, observing humans using tools or manipulating objects, Hayhoe and colleagues (Hayhoe et al., 2003; Mennie et al., 2007) found a close relationship of the concurrently performed action and the actor's gaze behaviour.

Generally speaking, human actors tended to fixate most of the time at the goal of the present motor act (Ballard et al., 1995; Pelz & Canosa, 2001). Spatial reaching errors reportedly increase if actors do not look at their targets (e.g., Bekkering, Adam, van den Aarssen, Kingmy & Whiting, 1995; Vercher, Magenes, Prablanc & Gauthier, 1994; Henrique, Klier, Smith, Lowy & Crowford, 1998; Neggers & Bekkering, 1999). Stritzke and Trommershäuser (2007) studied overt gazing behaviour during reaching under risk (i.e., while avoiding risky penalty regions) and found that saccades were determined by high-level, motor task-dependent factors that even outran saliency manipulations in the field. This may hint to the fact that visual preparation plays an outstanding role in the programming of the individual movement units.

Moreover, several studies started out to investigate the coupling of covert selective attention and the programming of simple reaching hand movements. Tipper and colleagues (Tipper, Lortie & Baylis, 1992), for example, tested the visual selection processes during the preparation of manual movements by placing task-irrelevant distracters in the field. They found that the distracters disturbed the visual preparation of the movement goal in that they prolonged the latencies of the reaches, but only if the distracters appeared along the movement path, i.e., between the starting position and the goal. Distracters that were presented in movement-irrelevant locations - e.g., well beyond the movement goal - were successfully ignored and had no effect on any movement parameter. When they further studied the kinematics of goal-directed reaches they found that the trajectories of the hand curved away from non-goal locations, indicating that these are inhibited by spatial attention (Tipper et al., 1997; Howard & Tipper, 1997). This was first, indirect experimental evidence for the notion that a visual distracter and the target compete for movement control if they are in a conflicting spatial relation. Further indirect evidence for the role of visual cues in the planning of hand movements came from studies of the effects visual context can have on the reach kinematics. Gentilucci and colleagues (Gentilucci et al., 1996), for example, let participants perform pointing movements from one end of a Muller-Lyer figure to the other. They found that subject overshot with their reaches if the illusory configuration was open, whereas they undershot the respective reach goal, if the configuration was closed. Deubel, Schneider, and Paprotta (1998) applied a more direct measurement of visual attention in a hand-reaching task. In a dual-task paradigm, participants had to execute a fast manual pointing movement to a centrally cued goal in the periphery without breaking central eye-fixation. As a secondary task, they had to discriminate a target letter (discrimination target), which was presented tachistoscopically during the preparation period at any position in the field. The target letter was either a digital 'E' or a '3', and the required perceptual task involved a 2-AFC discrimination. The results showed that the performance in the perceptual discrimination task strongly depended on the relative position of the movement goal. Discrimination of the target letter was superior if the goal for the manual reach and the discrimination target coincided at the same spatial location. If, however, the hand movement was directed to a different location discrimination performance dropped close to chance level. Paprotta, Deubel, and Schneider (1999) replicated these results with a circular arrangement of potential movement goals. Further, Eimer and colleagues measured event-related potentials in response to task-irrelevant visual transients and found that visual attention covertly shifts to the start position (but not the goal) of left or right hand if a respective manual movement was about to be programmed (Eimer et al., 2006; Van Velzen et al., 2006). Baldauf and Deubel (2009), however, also found electrophysiological evidence for beneficial visual processing at the intended goal location. Taken together, all these experimental studies reviewed so far leave little doubt that also manual responses employ visual selection of the intended goal location.

2.4 Parallel selection of multiple movement goals

Many goal-directed movements have to consider not only a single movement target, but require the processing of several locations or objects for movement preparation. Therefore, we recently extended these early results on the goal selection for simple, upcoming pointing movements by studying the deployment of visual attention during the preparation of more complex, sequential motor responses which involved several movement goals (Baldauf et al., 2006; Baldauf & Deubel, 2008; Baldauf & Deubel, 2009). In these studies, participants had to prepare rapid sequences of reaches to two (or three) peripheral goal locations. While maintaining strict ocular fixation at the centre of the screen the subjects first moved their index fingers to a location in the periphery that was centrally cued by a small arrow. Immediately after this reach, they moved on with a second reach along the circularly arranged elements to the next-but-one location (in a clockwise direction). They were instructed to perform this double-pointing movement as fast and as accurately as possible. Similarly to previous studies we used a secondary letter discrimination task in order to probe visual attention in the visual field during the movement preparation, i.e., shortly before the initial movement started. It turned out that the selective facilitation of task-relevant information was not restricted to a single upcoming movement goal. Rather, the data showed significantly increased discrimination performance at the first *and* second movement goal as compared to other task-irrelevant locations. Therefore, the visual attention system seems to be also involved in the preplanning of whole movement sequence in which several movement goals have to be reached serially. In experiments that required triple-sequences of pointing movements even the third goal was covertly attended well before the first reach component started (Baldauf et al., 2006; see also Baldauf & Deubel, 2008). Hence, also movement goals that lie in the rather remote future (i.e., at least some seconds ahead) are visually pre-selected if a fluent and rapid motor response is required. Ricker and her colleagues also examined the role of visual preparation in the execution of reaching sequences (Ricker, Elliot, Lyons, Gauldie, Chua & Byblow, 1999). A full vision condition was compared to conditions in which vision was eliminated during the execution of the first movement component. Their data suggest that the visual preparation of the second movement component is completed before the first movement is terminated and that vision prior to movement onset is used to configure a full movement plan to both targets.

Baldauf and Deubel (2009) added first physiological evidence for the parallel selection of multiple intended movement goals (Figure 1). They instructed the participants in their study to perform speeded double-reaches to two out of three peripheral locations. The first reach had to be directed to the middle cross of the configuration and the second reach had to be directed to the next position either in clockwise or counter-clockwise direction depending on the pitch of a go-signal, which was either a high- or low-frequent tone (see Figure 1A). The authors used a ‘dot probe’ paradigm to map visual attention in the workspace. For this purpose, a visual transient (i.e., a “dot probe”) was flashed during movement preparation at various locations in the visual field. The recorded event-related potentials revealed that visual transients at either the first or second goal location elicited bigger P1/N1-components in the ERP signal than the same visual stimuli at task-irrelevant locations (Figure 1B). This means that visual processing at the respective location in the visual field is enhanced.

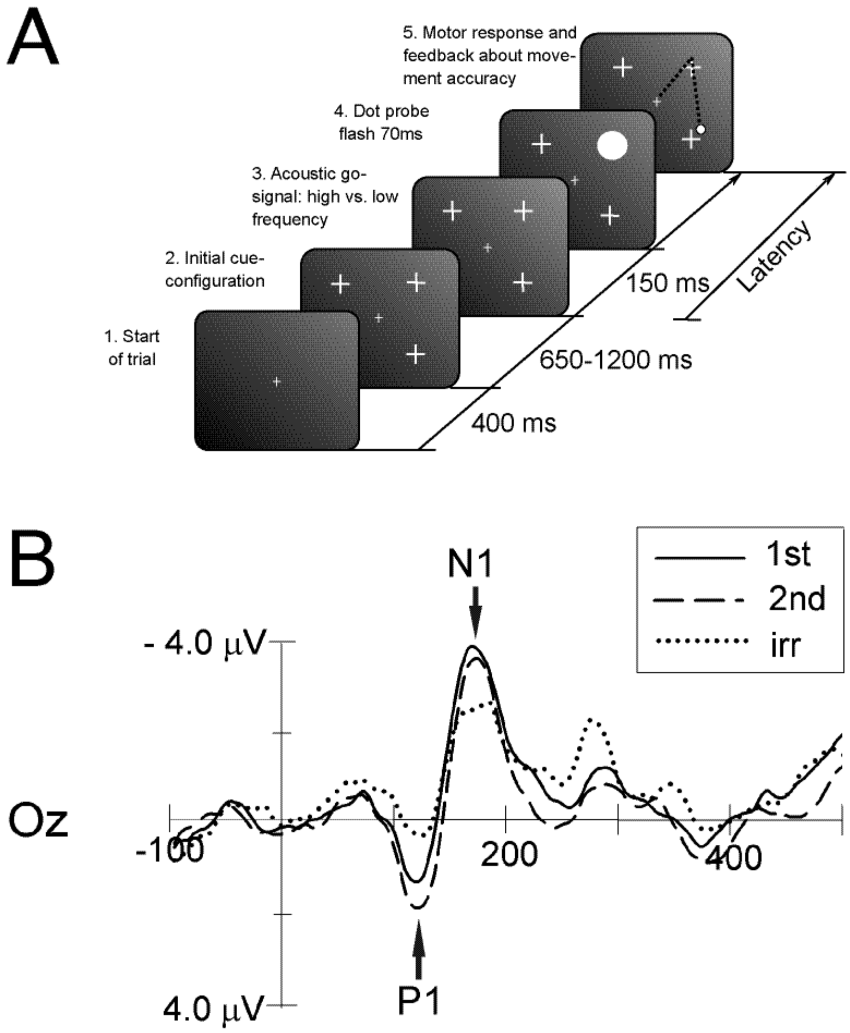

Figure 1. Selection of multiple reach goals. **(A)** Participants were instructed to always fixate at the central fixation cross. An initial stimulus configuration was presented consisting of three crosses (in the example here the configuration is oriented to the upper right quadrant). A high or low-frequent tone served as go-signal. Participants were required to execute a speeded double-reach with the first reach being directed to the middle cross of the configuration. Dependent on the pitch of the go-signal, the second reach led to the next position either in clockwise (low-frequent tone) or counter-clockwise (high-frequent tone). During movement preparation, at 150 ms after the onset of the go-signal, a task-irrelevant dot probe was flashed for 70 ms at one of the three cross locations. **(B)** Averaged event-related potentials evoked at an occipital electrode by the presentation of the dot probe. The dot probe could be flashed either at the first reach goal ('1st') or at the second goal ('2nd') or at the third, movement-irrelevant location ('irr'). Dot probes at either the first or second reach-goals elicited larger P_1/N_1- amplitudes than dot probes at irrelevant locations (Adapted from Baldauf & Deubel, 2009).

The finding that multiple movements in a sequence are prepared in advance is in line with recent studies investigating the chaining of movement components in everyday tasks like hand washing, tea making etc.

(e.g., Hayhoe, Shrivastava, Mruczek, & Pelz, 2003; Land, 2006. It became apparent that participants who were free to move their gaze prepare their movements several steps ahead by so-called look-ahead fixations. Studying covert attention shifts during action preparation likely provides additional information about ongoing selection processes. Naturally, the oculomotor system is a strictly serial system in that gaze can be directed to only one position in space at a given time. In contrast, covert attention turned out to be very flexible and parallel. When the participants of the study by Baldauf et al. (2006) were asked to prepare a sequential reaching movement, first to a centrally cued position and then to the next position in clockwise direction (see Figure 2A) it turned out that *both* intended goal positions were selected *in parallel*.

In this experiment, the authors implemented a letter comparison task as secondary task in order to test for the *parallel* selection of two sequential reach goals (Figure 2B). During the movement preparation, i.e., briefly after the presentation of the movement cue, two discrimination targets — both of them resembling either a ‘E’ or a ‘3’ — appeared at any two of the four peripheral positions. The remaining two positions showed other, irrelevant distracter letters (‘2’s and ‘5’s). After a presentation time of only 60ms all stimuli were masked. At the end of each trial the participant had to indicate whether both discrimination targets had been the same or different. Importantly, this letter comparison task in combination with the short presentation time excludes averaging artefacts and assures that the comparison of both discrimination letters can be successful only if both respective locations are selected simultaneously. The data indeed showed that the participants were able to compare the two discrimination targets within 60 ms if - and only if - both of these discrimination targets coincided with the two movement goals of the actually planned double-reach (Figure 2C). This speaks in favour of a *parallel* model of visual attention where visual resources are flexibly assigned to various locations in the field. Another interesting finding of this study was that the spotlight of attention split into multiple, spatially distinct attentional foci in order to select both future goal locations. When probing discrimination performance right in between both movement goals the perceptual performance was close to chance level just as it was at other task-irrelevant locations in the scene. This remarkable result shows that attention is dividable, at least under circumstances in which selection is employed in action preparation, and in which spatially accurate movements must be planned towards two distinct locations.

The view of flexibly adjusted visual resources in action preparation has been further supported by several studies that described a spatial gradient of attentional weights with more visual resources being deployed to positions that are more important from a motor-planning point of view (Baldauf et al., 2006; Baldauf & Deubel, 2008a; Baldauf & Deubel, 2008b; Baldauf, Cui & Andersen, 2008). When complex manual reach sequences require the parallel preparation of multiple goal positions it was observed that the immediate goals, i.e., the targets relevant for the impending movement, receive more visual attention than subsequent ones. In triple reach sequences for example this gradient followed an almost linear trend (Baldauf et al., 2006; Baldauf & Deubel, 2008a). Therefore, the deployment of visual attention during motor planning seems to reflect the required spatial *acuteness* as well as the motoric *instancy* (see also Ansuini, Grigis, Massaccesi & Castiello, 2008). In this respect, it may be noteworthy that Baldauf et al. (2009) observed that the relative weighting of the primary versus secondary movement goal was reversed when the behavioural difficulty of target acquisition was manipulated. When subsequent goals had to be acquired in remote future and no visual landmarks regarding the second goal location were given these secondary movement goals became rather hard to reach accurately. As a consequence, the representation of both movement goals in parietal populations reversed as well with even more resources being now deployed to the secondary goal as compared to the immediate one.

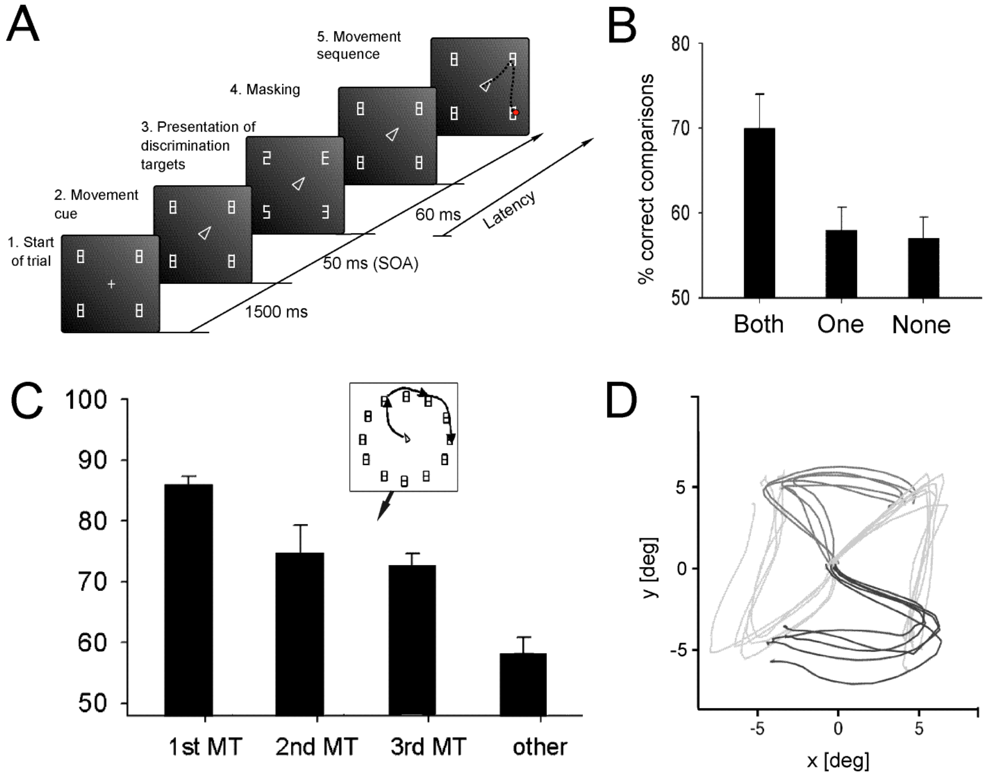

Figure 2. Parallel attentional selection of two goal sequential locations. **(A)** Participants were instructed to strictly hold central eye fixation and to perform speeded double-reaches to the centrally cued position and the next position in clockwise direction. In order to test for the parallel allocation of attention a secondary letter comparison task was employed. During movement preparation, two out of four elements changed for only 60 ms into discrimination targets (both resembling either a ‘E’ or ‘3’). At the end of each trial participants responded whether both discrimination targets had been the same or different. **(B)** Performance in the letter comparison task: the comparison was successful only if both discrimination targets coincided with the currently intended movement goals. If one or both discrimination targets are presented at movement irrelevant locations, the comparison failed. **(C)** In an experiment that required participants to perform triple-reaches, the discrimination of single target letters was increased at all three intended movement goals. The more remote the goal lay in the future the less attention was deployed to the respective position. **(D)** Trajectories of rapidly performed double-reaches to two out of four locations (Adapted from Baldauf et al., 2006).

In a follow-up study, Baldauf (2009) tested the visual preparation in reaching sequences as a function of the sequence timing. It was found that in rapid sequences with inter-reach delays shorter than 400ms a subsequent second goal was indeed preselected before onset of the movement sequence. In trials with longer inter-reach delays, however, the visual system solely prepared the immediate goal. This indicates that movement components are bound together and become integrated into one common action plan only if the delay between the movement components s short. Aivar and colleagues (Aivar, Brenner & Smeets, 2005; for the binding of action sequences on a different time scale see Ansuini et al., 2008) analysed the movement kinematics when human actors executed visually guided double-reach sequences in which sudden changes to the appearance of either the first or second target occurred during movement execution. They observed significant increases of the inter-reach dwell time and concluded that fast movement sequences are treated as a single action even if there is an intermittent target. In the field of movement kinematics, the phenomenon of "chunking" individual reaching movements that otherwise would lead to clearly separate goals into one common action plan has been often described (Adam, van der Bruggen & Bekkering, 1993; Adam, Paas, Eyssen, Slingerland, Bekkering & Drost, 1995; Adam & Paas, 1996; Khan, Mourton, Buckolz & Franks, 2007). Together, the findings demonstrate that the properties of attentional deployment reflect both timing and accuracy demands of complex movements in an amazingly specific manner.

Multiple movement goals occur not only in sequential actions but also, for example, when we manipulate objects bimanually. When studying visual attention in bimanual motor tasks it became again apparent that overt and covert attentional mechanisms may work together. For example, Riek and colleagues (Riek et al., 2003) investigated overt attention shifts in a task where they asked participants to reach bimanually to two locations. They observed a sequence of gaze shifts between both target locations until both index fingers finally landed on the respective goals. In a recent study, we probed covert attention by asking participants to execute very similar bimanual reaches while the eyes were on a central fixation and observed that both movement goals were attended in parallel (Baldauf & Deubel, 2008b). By comparing the perceptual performance at the goals of the left and right hand we found more visual attention to be deployed to the location that was farther away from the starting point and therefore was more difficult to reach. Also here, the pattern of attentional allocation seems to be sensitive to the specific demands of the motor task. Taken together, the results on sequential movements imply that for the selection of multiple movement goals it does not matter whether two movement components are executed simultaneously or serially as long as all the involved movement goals are behaviourally relevant during the preparation period.

Another example of a complex reaching task that involves multiple movement goals was recently studied by Collins and colleagues (Collins et al., 2008) who investigated visual attention in a reaching task involving tool use. They designed a triangularly shaped tool that subjects had to use to point to a goal location. The design of the experiment allowed to dissociate between the allocation of attention at the motor goal of the movement (i.e., at the end position of the effector) and at the spatial goal of the movement (i.e., the endpoint of the tool tip). Collins et al. showed that also in this task visual attention splits and selects in parallel both movement goals, the goal of the tool tip as well as the final position of the hand.

All these studies set the ground for analysing more complex aspects of visual movement preparation. They seem to imply that multiple movement goals do not overburden the visual system because covert attention mechanisms can – in contrast to the oculomotor system – select several areas in parallel if required by the motor task.

Also the quantitative relation of attentional resources that are allocated to the various goals was shown to be flexible in respect to the motor task demands. Of course, however, we cannot prepare arbitrarily many movement goals at once. Clearly there must be a limit. Therefore, the fact that several intended movement goals (i.e., at least three of them) are prepared in parallel by multiple foci of visual attention is very fascinating also from another point of view: For quite a while researchers have put forward the hypothesis that visual attention and working memory are interrelated functions. Smith and Scholey (1994), for example, argue that the maintenance of spatial memory involves covert shifts of attention (see also Smith, 1996). Also Awh et al. (1998) tested the proposed relationship and indeed observed facilitated visual processing at the location they had to hold in memory. However, it was Baddley and his co-workers (1987, pp. 116-121) themselves who first conceptualized a connection between the rehearsal in working memory and hidden action plans: In their influential working memory model (1987) they proposed for the first time that the spatial component of visual memory (the so-called visuo-spatial sketchpad) may be based on the implicit preparation of eye movements: ”preliminary evidence seems to implicate an eye movement or visual attention system as playing a role in this type of memory (i.e., the visuo-spatial sketchpad)” (Baddeley, 1987, p. 143). In the meantime many experimental studies followed this idea and proved strong similarities between attention and working memory. For example, Awh et al., (2000) showed that task-irrelevant visual transients elicit very similar event-related EEG-components whether participants are involved in a spatial attention task or a spatial memory task (further studies are reviewed by Awh and Jonides, 2001). Also physiologically the involved networks seem to overlap to a considerable degree (see below in the section on the neural substrate of selection-for-action). This striking connection between visual attention and visual working memory is further supported by the experiments of Smith & Pelky (1992) who demonstrated that spatial working memory is affected by goal-directed manual reaches. Given what we know about working memory and given what we have so far learned about visual attention in action preparation, we can deduce the hypothesis that there is likely a maximum ‘magical number’ of movement goals that can be prepared by visual attention in parallel, namely about four.

2.5 Visual preparation of grasps

Grasping an object seems to be a trivial task that at least adults perform with ease. But considering the fact how long it takes humans to optimize these skills may give a hint that visually guided grasping is not an easy but highly complex type of action (Kuhtz-Buschbeck et al., 1998; Schneiberg, Sveistrup, McFadyen, McKinley & Levin, 2002; Rösblad, 1996). Stable grasps, i.e. grasp types that are appropriate to the respective object and avoid collisions etc., are a largely unsolved problem also in the field of robot engineering, particularly if the sensory information is restricted to (binocular) visual input (Corke, 1993; Hasimoto, 1993; Hauck et al., 1999; Schenck et al., in press). With respect to selective visual processing, grasping is quite a challenging task since here again multiple movement goals - the future points of finger application - need to be prepared. Smeets and Brenner (1999), for example, emphasized this point by a model that conceptualizes grasping to be the same as pointing with the thumb and index finger toward selected positions on the surface of an object. Another aspect that makes visually based grasping more challenging as compared to simple reaching is the fact that additional information about the object’s features, such as its presumed weight, its point of gravity etc., becomes relevant during grasp preparation. Finally, visual attention again comes into play at the very end of the movement when visual feedback needs to be integrated for final movement control (Binstead et al., 2001; Lünenburger et al., 2000).

Johansson and co-workers were among the first to study overt selection during grasping (Johansson, Westling, Bäckström & Flanagan, 2001). Their participants initially had to grasp a bar and then to use it in on order to press a switch without colliding with an obstacle along the transportation path. Similarly to the findings regarding gaze behaviour in more natural tasks (Land & Hayhoe, 2001; Aivar, Hayhoe, Chizk & Mruczek, 2000; Hayhoe, 2000; Land, Mennie & Rusted, 1999) the Johansson et al (2001) reported that actors always directed their gaze to positions they were about to make contact with, such as the application point on the bar or the final movement target. Locations which they had to actively avoid, like the obstacle, were also fixated in almost every trial. However, with respect to the grasping component, Brouwer et al. (2009) pointed out that in the task setup of Johansson et al. only one point of application was visible to the actor, the second contact point was hidden in the back of the object. From this point of view, the study of course cannot resolve the question which surface parts of an object are visually selected before or during grasping movements. In a recent study, Brouwer and her colleagues (Brouwer et al., 2009) further investigated the fixation behaviour of human actors during grasping under conditions where all potential points of application were clearly visible to the actor (see Figure 3A).

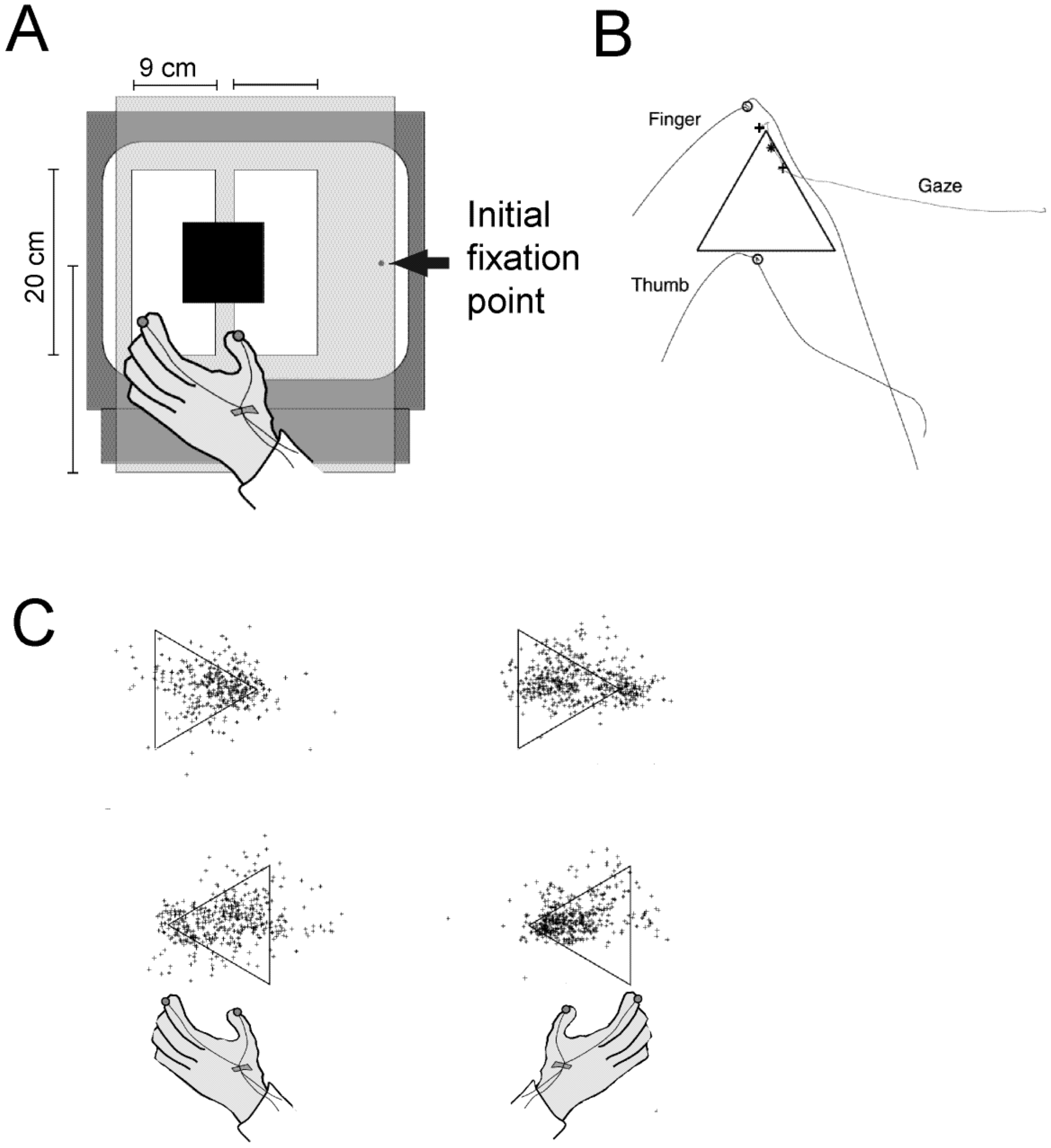

Figure 3. Overt selection of to-be-grasped objects. **(A)** Apparatus used by Brouwer et al., 2009, for studying the gazing behaviour during visually guided grasping of geometrical objects. At the very beginning of every trial an initial fixation point was presented to the left or right of the to-be-grasped stimulus. **(B)** Example of the gaze orientation when grasping an upright triangle. The eyes preferentially select the intended contact point of the index finger at the top of the shape rather that the thumb's goal location. **(C)** In their second experiment, Brouwer et al. instructed participants to grasp objects either with their right or left hand. The spatial pattern of eye fixations that accompanied the grasping movement indicates that there is a tendency to covertly select the smaller of two application locations (e.g., the tip of an triangle) where the contact with the object needs to be more precisely. (Adapted from Brouwer et al., 2009).

One particularly interesting result of their study was that open fixation behaviour in a grasping task becomes different from gaze control in a free-viewing conditions without grasping as early as for the second saccade in a trial (which is usually completed long before the hand touches the object's surface). Interestingly, the authors also exploited the fact that the initial fixation can select only one of the two points of interest (the application points of index finger and thumb) and tried to dissociate gaze behaviour in service of target selection from gaze behaviour aiming at the optimisation of visual feedback of the approaching hand. To do so, they relied on the fact that thumb and index finger presumably play functionally different roles in precision grasps: previously it had been be shown that the thumb generally guides the hand to the object, as can be seen in the straight trajectories (Galea et al., 2001; Haggard & Wing, 1997). In contrast, the index finger seems to be used in order to regulate the hand's aperture during the final grasping phase, as can bee seen from its more curved and more variable trajectory (however for a different model see Smeets and Brenner, 1999, 2001, 2002). From these kinematic findings, one would expect that more visual feedback is needed at the index finger's point of application whereas the thumb's goal requires a greater degree of target selection. Indeed, Brouwer and co-workers were able to show that eye gaze landed consistently at the planned contact point of the index finger, rather than at that of the thumb (see Figure 3B). They hardly observed any gaze switching between both locations. In a second experiment, they had participants grasp geometrical shapes with either their right or left hand. Here, participants preferentially fixated those contact points which were more difficult to make contact with, e.g., the smaller tip of a triangle (see Figure 3C).

These findings provide strong evidence for the hypothesis that overt eye movements in grasping preferentially select those object parts at which visual feedback is needed (see also Binstead et al., 2001, deGrave et al., 2008). But as the authors pointed out, the gaze can only be at one location at a time and the time needed to complete the reach-to-grasp movement is probably not sufficient to sequentially scan the object's surface efficiently. Therefore, it may be asked which positions of a to-be-grasped object are selected *covertly*, possibly several of them in parallel. Interestingly, in Brouwer et al.'s study also the centre of gravity (COG) of the object had an effect on the distribution of gaze landings. The initial saccade to the object for example was always biased towards the COG as often observed in pure object inspection (without any motor task). Also, many secondary saccades were still biased towards the COG. This may indicate that also the COG – because of its high behavioural importance for the following manipulation of the object — was attended covertly and therefore biased these saccades. For example, it has been shown that precision grasps are only stable if the COG lies between both points of application (Iberall et al., 1986; Mac Kenzie & Iberall, 1994)

Only very few studies have probed *covert* visual attention; they support the hypothesis that there is more selected of a to-be-grasped object than just one of (at least) two points of finger application. In a dual-task paradigm, Castiello (1996, 1999) let subjects grasp fruits and simultaneously count how often a peripheral distracter object was illuminated. He observed that the size of the distracter influenced the maximal aperture of the ongoing grasp movement. In trials without the secondary counting task, subjects successfully ignored surrounding distracter fruits and the hand movement kinematics remained unaffected (see also Castiello, 2001). Craighero, Fadiga, Rizzolatti, and Umilta (1998) reported that even task-irrelevant pictures of objects could prime the preparation of grasping movements. Subjects performed the grasps faster if they saw a picture of the same objects that they had to grasp for. The authors found similar priming effects for the orientation of graspable bars (Craighero, Fadiga, Rizzolatti, Umiltà, 1999). However, such general visuomotor priming effects on visually guided grasping movements were hard to replicate in the following (Cant, Westwood, Valyear & Goodale, 2005). In a study by Bonfiglioli und Castiello (1998) participants had to covertly track a moving distracter in the periphery while grasping for a target object. The allocation of covert attention to the moving stimulus affected the transport component of the reach-to-grasp movement. In a subsequent experiment, Kritikos, Bennett, Dunai, and Castiello (2000) varied the size of the distracter that had to be attended covertly and found that the distracter's size also interfered with the manipulation component of an ongoing grasp, in particular with the maximal aperture of the hand.

Schiegg and colleagues (Schiegg, Deubel, & Schneider, 2003) directly probed the spatial and temporal properties of covert visual attention when observers were required to grasped a wooden cross with their thumb and index finger (see Figure 4 A). The participants were not allowed to break gaze fixation from the object's centre. Via a mirror setup visual probe stimuli were projected into the action plane and changed into discrimination targets during the movement preparation period. Upon a go-signal, participants had to grasp the cross either with their right or left hand, depending on the pitch of the imperative stimulus. When using the right hand, the thumb touched the lower left branch end and the index finger touched the upper right branch end. When using the left hand the respectively opposite branch ends had to be contacted. Shortly after the go-signal with an SOA of 150 ms one of the projected mask elements changed into a symbol resembling either an E or a 3 whereas all other mask elements changed into irrelevant distracters. All probe stimuli were post-masked after 140 ms, i.e., well before the actual reach-to-grasp movement started. After completing the appropriate grasp participants had to indicate whether they had identified an 'E' or a '3'. The discrimination performance in this secondary letter discrimination task served as a measure for the deployment of visual resources in the field of action (see Figure 4 B). The results revealed a significantly enhanced discrimination performance in those trials in which the discrimination target was presented close to an intended point of application compared to trials in which the discrimination target was presented at the opposite, not-grasped ends of the object branches. Perceptual performance at both points of application was improved compared to control experiments in which no grasping movement had to be executed. The spatially selective processing at intended application points could be observed even if the subject was informed about the location at which the discrimination target was to be presented. This was interpreted as evidence for an obligatory coupling of prehension movement preparation and visual attention: It is hardly possible to attend to certain surface patches on an object while preparing a grasp movement to other target zones on the very same object. Interestingly, this study shows (in some contrast to the overt selection processes that Brouwer et al., reported during grasp preparation) that both points of application were selected covertly. These results fit into the picture that covert attention can be split and flexibly arranged to the needs of the current motor task – much better than overt selection by the oculomotor system can.

Presumably, what is usually referred to as 'grasping' comprises distinct phases of an action. For example, grasping an object starts with a reach-to-grasp movement (or 'transport phase', see e.g., Bonfiglioni & Castiello, 1998) that brings the hand close to the object of interest, followed by — or passed into — a second phase in which the appropriate grasp type is formed and the movement is piloted to the points of application (Smeets & Brenner, 1999 termed this the 'grip component'). In a manipulation phase, finally, the grasp is stabilized and grip forces are continuously adjusted to compensate for the changing forces of gravity. Along this evolving temporal succession visual attention could play different roles such as target selection for the initial reach component, followed by the selection of more specific application points, and finally the selection of relevant object features such as its centre of gravity. Droll and colleagues for example studied change detection in various stages of a virtual manipulation task (Droll, Hayhoe, Triesch, & Sullivan, 2005). They found that the actors' ability to detect changes to the visual appearance of the currently manipulated virtual objects altered dramatically over various manipulation phases such as the pick-up, the transportation, or the put-down of objects. Future studies of covert visual attention in grasping are required that focus on the temporal dynamics and the continuously changing function of visual selection processes during the course of the grasp.

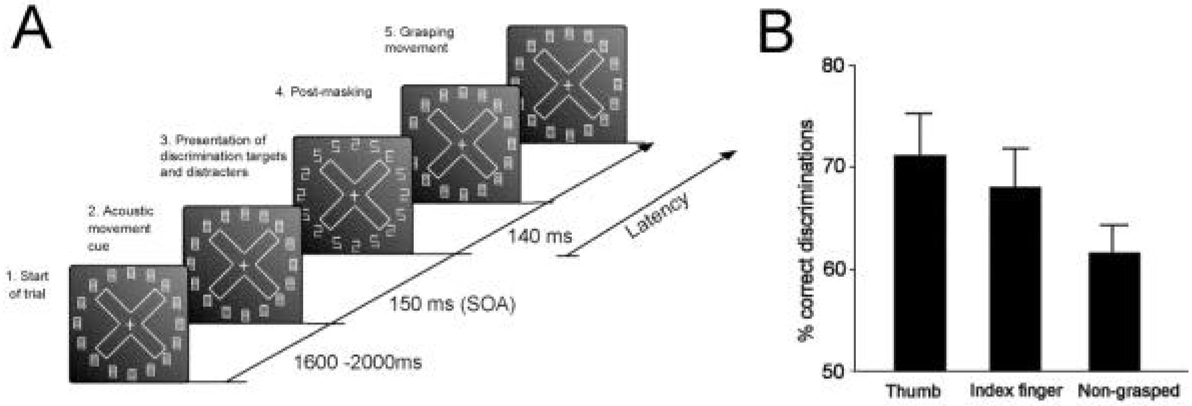

Figure 4. Covert selection of to-be-grasped object parts. **(A)** Sequence of stimuli in an experiment by Schiegg et al. (2002) to map visual attention at various surface points of a cross-shaped, to-be-grasped object. Just before the reach-to-grasp movement is initialised, i.e., only 150ms after the onset of the go-signal, a discrimination letter ('E' versus '3') is briefly presented at a random position among distracters ('2's and '5's). At the end of the trial, after the grasp is completed, participants have to respond whether an 'E' or a '3' had been presented during movement preparation. The discrimination performance at the various position serves as measure for the allocation of visual attention. **(B)** Discrimination performance at both intended points of application for the thumb and index finger were superior to the discrimination performance at other, currently not intended points of application

2.6 Reaching and grasping in cluttered scenes: avoiding obstacles

In natural tasks, we usually do not act on isolated objects but often in cluttered or even crowded visual lay-outs. Especially during the initial reach-to-grasp component, the presence of an obstacle poses an important additional burden for the visual preparation and the motor programming of a successful grasp. Depending on their physical features, their position relative to the movement goal, and their visual appearance other, non-target objects can be conceptualized as mere distracters that detract attention from the current goal. Distraction can either result from competition for visual processing (e.g., Castiello, 1996, 1999; Tipper et al., 1997; Tipper et al., 2002), or be due to the fact that obstacles need to be actively avoided and ere therefore integrated into the action plan (Tresilian, 1998, 1999; Mon-Williams et al., 2001; Tresilian et al., 2005). Tresilian (1998) emphasized that non-target objects in movement tasks often do not fit the definition of ‚distracters' because they are in many cases not irrelevant to the task but constitute spatial constraints on the execution of the reach. He showed that people generally keep their hands outside of a region that surrounds the obstacle by a minimum preferred distance (see also Dean & Brüwer 1994.

Tipper and colleagues similarly described an 'attentional repulsion' effect by showing that reach trajectories deviate away from non-target objects that were attentionally inhibited (Tipper, Howard & Jackson, 1997, Howard & Tipper, 1997). Interestingly, they could demonstrate that hand movement trajectories also curved away from purely visual stimuli without noteworthy physical extension such as an illuminated LED (see Figure 5 A). These stimuli arguably do not obstruct the approaching hand (see also

Gangitano et al. 1998; Jackson et al. 1995; Meegan & Tipper 1998; Pratt & Abrams, 1994; Saling et al. 1998). Based on the effects non-target objects had on the kinematics of simple reach movements, Tipper and colleagues (Tipper et al., 1997) proposed that the involved attention system must represent more than just the target object for action. To move the hand around or over an obstacle requires an internal representation of the obstacle. They suggested that obstacles do not only have to be ignored but that they automatically afford alternative action plans that compete with the actual goal of the intended reach. These competing internal representations of non-goals are inhibited in real-time, causing the hand to curve away from the non-target object. Similarly to the results of Tipper et al., Chapman and co-workers found stronger activation of reach-related areas in the parietal cortex (specifically in the precuneus, the human homologue to the parietal reach region in monkeys) when non-target objects were present during reach movements. Together, the various results suggest that non-target objects (independent of whether they constitute physical obstacles) strongly influence the attentional preparation as well as the execution of reaches and grasps.

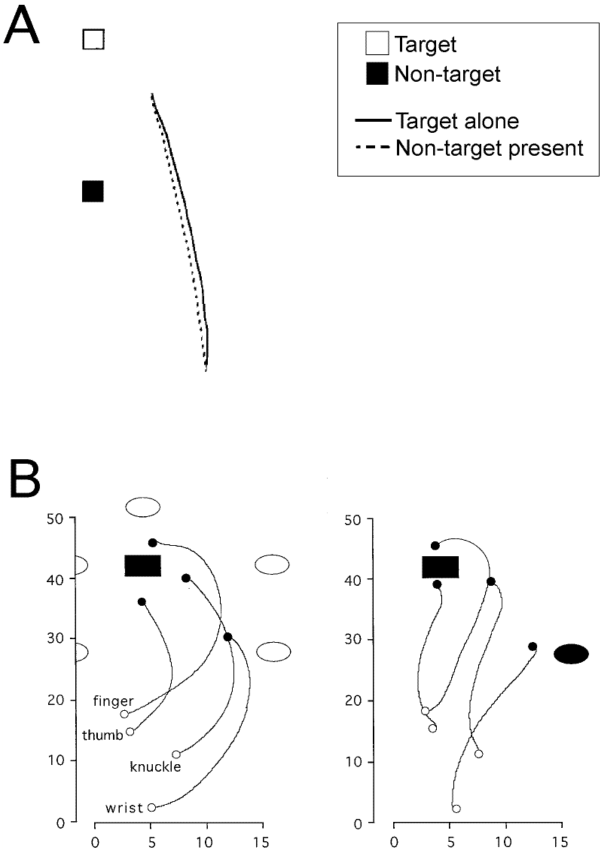

Figure 5. Movement trajectories in the presence of non-targets. **(A)** Trajectories curve away from non-targets and visual distracters. According to Tipper et al. (1997) this is the effect of alternative, though inhibited, action plans, which are automatically afforded by the non-target stimuli. **(B)** In a study by Tresilian et al. (1998) participants had to grasp for a target object either without obstacles (left) or with obstacles present in the workspace. According to Tresilian et al., obstacles constitute spatial constraints to the hand path, which has to be adjusted accordingly keeping the hand outside a minimum distance. (Adapted from Tipper et al., 1997 and Tresilian et al., 1998).

Using grasping tasks, several studies have shown that the initial reaching component takes longer if an obstacle is present as compared to the same movement executed without any obstacles (Biegstraaten et al. 2003; Jackson et al. 1995; Jaric et al. 1999; Mon-Williams & McIntosh 2000; Mon-Williams et al. 2001;

Saling et al., 1998; Tresilian, 1998), which can be taken as evidence for the additional need of anticipatory programming. Also the maximum grip aperture during the initial transportation phase was shown to be smaller when the grasping movement was performed around an obstacle (Jackson et al. 1995; Mon-Williams et al. 2001; Saling et al. 1998; Tresilian 1998). Presumably, closing the moving hand is a clever strategy to minimize the risk to collide on flight with the obstacle.

The behavioural significance of obstacles is also reflected in the open gaze behaviour. Obstacles are usually fixated while the hand moves around them. For example, Johansson and colleagues (2001) found that an obstacle was fixated on 80% of the trials when actors manoeuvred a bar around it. When participants were required to fixate elsewhere, the hand collided more often with the obstacle.

Deubel and Schneider (2004) measured how visual attention is covertly deployed to a central obstacle immediately before reach initialisation. By instructing a reach with either the right or left hand towards a goal at either the right or left upper quadrant of the workspace, they manipulated on a trial-by-trial basis how task-relevant, i.e., how obstructing, a central obstacle was. For example, the central obstacle was highly obstructive when the right hand had to reach to the upper left goal position, whereas the same obstacle was hardly relevant when the right hand had to reach to the upper right goal. The allocation of visual attention in the scene was measured by a secondary perceptual task in which the subjects had to discriminate briefly presented letters that were flashed during the movement preparation at either the movement goal or at the location of the obstacle. In those trials in which the central object was obstructive, discrimination performance at the obstacle's position was significantly enhanced in comparison to trials without obstacles or trials in which the central object was not obstructive to the planned movement. These results indicate a preferential processing of visual information not only at the movement goal but also of the obstacle. They suggest that an obstacle is visually selected during movement preparation if the actor is required to avoid it.

The reported effects of non-target objects on the kinematics of reaching movements together with the studies demonstrating facilitated visual perception at the location of obstacles show that not only the final goal location of a reach is selected by visual attention, but also non-targets, given they are movement relevant.

The importance of visual attention for the successful avoidance of obstacles in reaching tasks also becomes evident in neuropsychological studies. Not surprisingly, some human patients with parietal lesions experience tremendous problems when they have to reach around or over an obstructive object. Schindler and colleagues, for example, describe two patients with optic ataxia who did not exhibit normal obstacle avoidance (Schindler et al., 2004). While control participants adjusted their reaching trajectories to the variable position of two obstacles, the patients kept performing reaches along the same direct trajectory and completely ignored the obstacle configuration.

For a more detailed understanding of the selective processing in obstacle avoidance, it remains to be investigated which parts or aspects of an obstacle are selected by covert and/or overt attention. For example, it has not been studied so far whether attention is specifically focussed on the obstacle's border or rather on the whole object. Similar to the questions that remain for the selection of to-be-grasped goal objects, it may be fruitful to analyse in more detail the flexible distribution of (overt and covert) visual attention on objects that function as obstacles for the movement.

2.7 Neurophysiology of attention in reaching and grasping

The interplay of visual attention and visual guidance of movements is reflected in the fact that both functions share common neural structures. In the following, we will review studies that document the prominent role of the posterior parietal cortex in the selection-for-action for both reach and grasp movements. Again, we will put a special focus on how this structure aids to the preparation of those more complex actions that involve multiple movement goals.

The posterior parietal cortex (PPC) has traditionally been investigated with regard to its role in visually guiding movements (Glickstein, 1996; Hyvärinen, 1982, 73; Mountcastle et al., 1975). Monkey physiology has identified various substructures of PPC – all clustering around the intraparietal sulcus (IPS) – that encode in parallel spatial information for different effectors (He & Andersen, 2007; Snyder et al. 1997, 2000; Andersen & Buneo 2002; Andersen et al. 1997; Konen et al. 2004; Rizzolatti et al., 1994; Graziano & Gross 1994, see Figure 5A). The lateral inferior parietal cortex (LIP), for example, has been shown to be specifically activated during the preparation of saccadic eye movements (Colby et al., 1996; Sereno, Pitzalis, & Martinez, 2002) as well as during covert shifts of attention (Chelazzi & Corbetta, 2000, Colby, 1998; Colby & Goldberg, 1999).

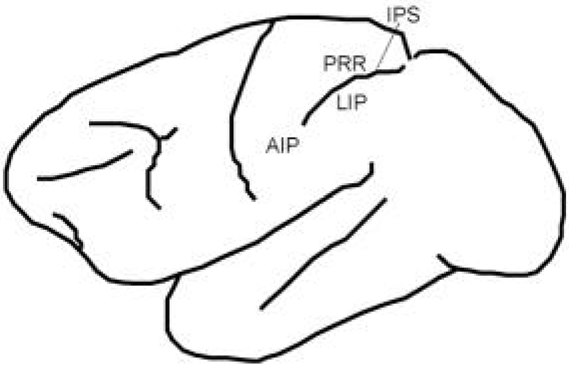

Figure 6: The posterior parietal cortex (PPC) plays a crucial role in the transformation of visual input into movement plans for reaching and grasping as well as in the attentional selection of visual stimuli. A mosaic of functionally specialized areas cluster along the intraparietal sulcus (IPS): the lateral intraparietal area (LIP), which is specifically activated before saccadic eye movements; the parietal reach region (PRR) which is selective for the planning of arm reaches; the anterior intraparietal area (AIP) plays a crucial role in the adjustment of hand postures for upcoming grasp movements.

More relevant to the preparation of hand movements, however, is the parietal reach region (PRR), which in monkeys is roughly located along the medial bank of the IPS and area V6. Neurons in PRR were specifically activated before reaching movements and have therefore been interpreted as encoding reach intentions (He & Andersen, 2007; Buneo & Andersen, 2006; Calton et al., 2002; Snyder, Batista, & Andersen, 1997, Taira et al., 1990). Neuronal circuits within PRR identify and interpret visual goals for hand movements (Scherberger et al., 2007). Also they help transforming the retinal position of a target in respect to the line of gaze into other, motor-relevant frames of reference such as the directional information that guides the hand to the goal (Buneo et al., 2002). Neuroimaging studies in humans found a possible homologue of PRR in the human IPS (Conolly et al., 2000; DeSouza et al., 2000; Kertzman et al., 1997).

Binkofski et al. (1997) showed in humans that a more anterior area within PPC — the anterior intraparietal area (AIP, see Figure 5A) — is typically activated during visually guided grasping (see also Culham, 2003; Culham et al., 2003; Castiello, 2005; Culham & Valyear, 2006; Shikata et al., 2008). In further fMRI studies this patch of human cortex turned out to also be sensitive to the mere presentation of graspable objects (Chao & Martin, 2000). Tunik et al. (2005) fostered the view that AIP is involved in the pre-shaping of the grasping hand. When they applied TMS to the anterior part of IPS the participants were no longer able to accurately adjust the hand posture to sudden changes in the orientation of the to-be-grasped object. The effect of the TMS application was restricted to AIP, stimulation at more dorsal parietal or parieto-occipital sites did not hamper grasping movements (similar to Glover et al., 2005). In humans, lesions to the PPC often cause disorders also in the planning and execution of goal-directed hand movements, e.g., limb apraxia and optic ataxia (see Balint, 1909). Lesions that cause optic ataxia in humans always include the IPS and sometimes involve parts of the inferior or superior PPC (Culham & Valyear, 2006). Karnath and Perenin (2005) compared many case studies of optic ataxia and found the IPS and adjacent regions to be commonly activated.

Most importantly, there is also the second prominent function of the posterior parietal cortex: it is widely agreed that the posterior regions of the parietal cortex (PPC) play a crucial role in shifting spatial attention. In human and non-human primates, attention-related activations has been observed throughout the posterior parietal cortex on the level of individual cells (e.g., Colby & Goldberg, 1999; Rushworth et al., 2001; Corbetta & Shulman, 2002; Bisley & Goldberg, 2003) as well as on the level of metabolic activity of whole brain areas (see, e.g., Wojciulik & Kanvisher, 1999; Corbetta et al., 2000; Perry and Zeki, 2000; Corbetta et al., 1998; Corbetta et al., 1993; Giesbrecht et al., 2003; Yantis et al., 2002). Shikata et al. (2003) found a gradually increased BOLD signal in the anterior IPS (a proposed homologue to non-human AIP) when they compared an attentional task, namely the visual discrimination of surface orientation, with the imagination of a grasping movement as well as with the actual execution of a grasp movement. This double function of the PPC demonstrates how perceptual attention and action preparation are linked in terms of neural substrates.

What about complex movement tasks that afford multiple activation foci? Barash (1996) pointed out that the neuropsychological syndrome of extinction gives a strong hint to the involvement of the parietal cortex in the representation of multiple areas of interest. Patients who suffer from extinction after lesions to the PPC are unable to apprehend two stimuli presented simultaneously in the left and right hemifield. Milner (1996) described extinction therefore as a pathological attentional bias to the ipsi-lesional field (in the sense of a biased competition model, see Desimone & Duncan, 1995). This suggests that the PPC in healthy humans is essential for the apprehension of two simultaneously presented stimuli. Courtney et al. (1996) showed in a PET study that SPL was bilaterally activated by a working memory task in which participants had to remember three locations in the visual field. Todd & Marois (2004) used fMRI and showed that activity in the posterior parietal cortex correlates with the amount of spatial information that is stored in VSTM (see Figure 6 A). Therefore, PPC has the capacity to simultaneously represent multiple locations in space.

Recently, Baldauf, Cui, and Andersen (2008) recorded from single neurons in the PRR while the animals were preparing for a double reach task to two peripheral goal locations (see Figure 6B). After mapping the response fields of single units in PRR they placed either the first or the second goal of a reach sequence in the response field of a cell. By analyzing the neuronal activity during a memory-period, which ensued between the presentation of the movement cues and the go-signal, they were able to attribute the cell's planning activity to the representation of either goal position. Most of the cells within PRR encoded immediate goals and subsequent goals equally well. This implies that PRR encodes multiple movement goals of a planned hand movement sequence in parallel. Given that PRR has a retinotopic organization (Swisher et al., 2007), it was argued that the eye-centered planning activity in PRR is a likely source of attentional top–down signals that facilitate visual processing at multiple goal positions.

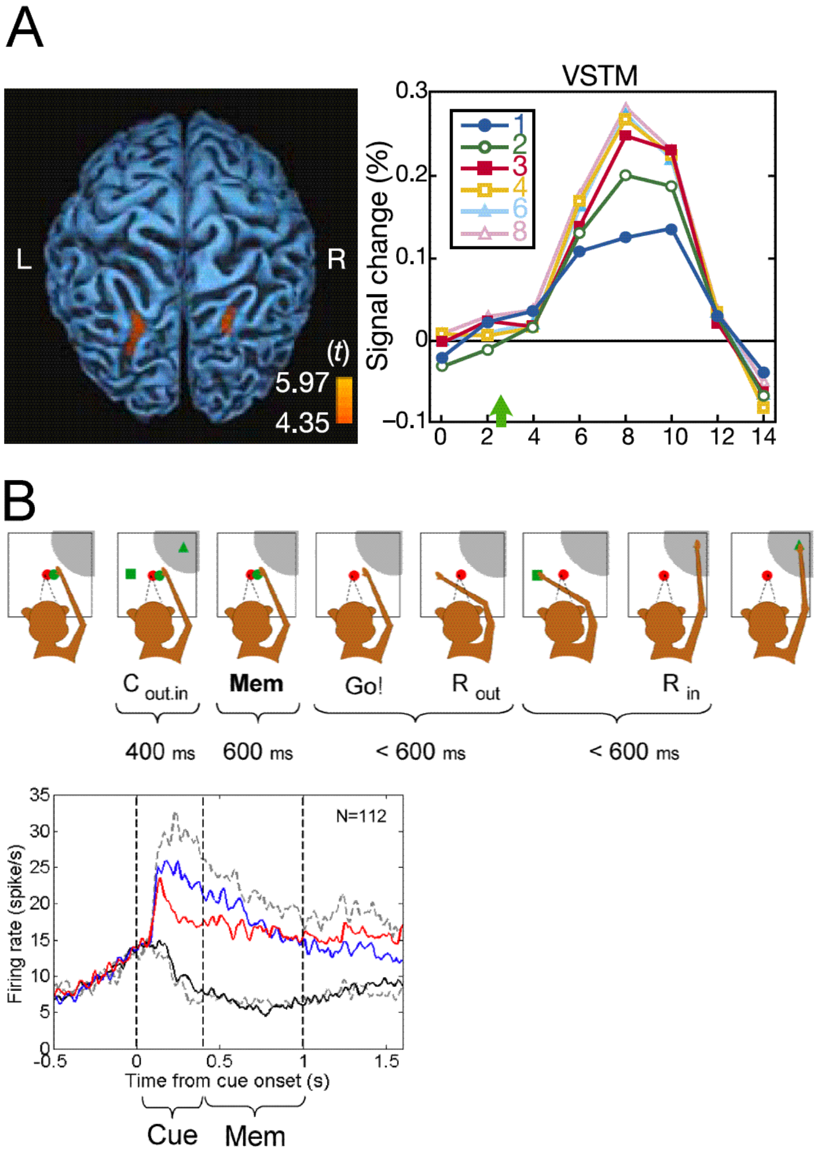

Figure 7: **(A)** The activity in the posterior parietal cortex reflects the load of the visual working memory. The more items have to be remembered in the memory task, the stronger activated was the PPC. (Adapted from Todd & Marois, 2004). **(B)** Sequential double-reach task used by Baldauf et al. (2008). During the memory period PPR neurons prospectively represented the first and second movement goal to about the same extent. (Adapted from Baldauf et al., 2008).

Functionally, the output of neural populations in the PPC could be projected in two directions. Whereas the encoding of movement intention is passed to further motor-related structures in the frontal brain, the very same output could be back-projected (top-down) to early visual areas and subserve the selection-for-action. The reach- and grasp- related structures within the PPC “seem to do double duty” (Milner, 1996) and mediate the interconnection of both functions in the sense of the premotor theory of attention (Rizzolatti et al., 1984).

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Chapter 3

Kinematics of human grasping

3.1 Objectives

In an extended investigation with human participants we studied in which way different hand postures taken at the start of the movement affect the kinematics of the grasp (Attachment 1). So far, very little attention has been paid to the effects of varying the starting posture of the hand on grasping kinematics although in everyday life we rarely start grasping with the hand aligned to the body midline and all fingers pinched together, as done in most grasping studies. Accordingly, the classical experimental grasping task required that participants begin their grasping movement with all fingers pinched together at a given starting location which is often aligned to the body midline or slightly to the right of the participants' body. From these studies it is well known that: (a) the size of the object strongly influences the grasp component such as the maximum grip aperture and its timing, (b) the position and the distance of the target object primarily affect the transport component of the movement such as movement time and peak velocity, and (c) that the orientation of the object changes the kinematics of both components, transport and grasp, hence hand orientation was sometimes considered to constitute a third (independent) component of the grasping movement. However, it is still a matter of debate whether the components of transport and grasp are independent of each other. Whereas studies using simple grasping tasks are in favour of two (or three) independent visuomotor channels which are merely temporally coupled (Jeannerod, 1984; Arbib, 1981), studies using more complex grasping tasks give evidence for the interdependence of all components (Paulignan et al., 1997; Desmurget et al., 1996). In addition, there are studies which are in favour of a *spatial* coupling of transport and grasp component (e.g., Haggard & Wing, 1998; Rand & Stelmach, 2005). So, it may be that the assumption that grasping is a relatively stereotyped movement pattern might be due to the fact that the movements were primarily investigated using a simple, standard grasping task.

The aim of this series of experiments was to examine the changes in grasping kinematics resulting from a change of the starting posture of the hand. We were especially interested in the way in which and over what time course the grip is adjusted to the object's properties. Furthermore, we wanted to investigate how the different components of the movement (transport and grasp) were affected and whether their temporal and/or spatial coupling persists if the initial start posture is changed. For this purpose, participants had to grasp objects of different sizes starting with the fingers pinched together, slightly open, widely open, or fully stretched. We also varied the orientation of the grip at movement beginning, and participants had to grasp a cylinder which was presented at different positions. Thus, this study adds to the understanding of human grasping in more complex and natural situations.

3.2 Results and discussion

The results show that the grasping kinematics of the human hand changes considerably if the starting posture is varied. The data reveal a complex pattern of closing and reopening of the hand aperture that occurs not only when the fingers are fully stretched but also if fingers were slightly open and had to open further to grasp the object successfully. We also found considerable changes in both transport and manipulation components when the starting orientation of the hand was varied. The variation of the start orientation was not only associated with a change of the finger position in space, but also with a change of the hand position and the rotation of the wrist. Since the selection and adjustment of the finger opposition axis determines the position of the hand in work space, it seems very unlikely that the hand orientation constitutes a third independent movement component besides reach and grasp. Regarding the coupling of transport and grasp, our results neither support a fixed temporal nor a fixed spatial relationship of both components. We could show that the timing of maximum grip aperture within the movement time also depends on the start posture of the hand. Besides, it was proposed that the temporal linkage between grasp and transport consists in a high correlation between relative time to maximum grip aperture and the relative timing of peak deceleration of the wrist (Jeannerod, 1984). However, in our data we found very few correlations between these two variables which suggests that this relationship may change with task demands. Thus, none of the models in grasping based on an invariant temporal or spatial coupling of both components can account for our results.

Rather, the results show that the more complex the alteration of the start posture, the more the kinematic parameters involved were affected by these start conditions. Overall, the findings suggest that the motor system plans an economical and efficient movement taking the actual start posture of the hand into account.

Attached papers

A Changes in grasping kinematics due to different start postures of the hand, C. Hesse and H. Deubel, Human Movement Science, (in press)

Changes in grasping kinematics due to different start postures of the hand.

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February 25, 2009

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RUNNING HEAD: ”Grasping with different start postures”
keywords: grasping, perturbation, posture, kinematics, motor control

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Abstract

It was proposed that grasping is a relatively stereotyped movement pattern which can be subdivided into the components of manipulation, transport and orientation of the hand. However, it is still a matter of debate whether these components are independent of each other. In three experiments we altered the start posture of the hand by either changing the size of the start aperture or the orientation of the hand prior to movement onset. The variation of the aperture size primarily affected the manipulation component of the grip resulting in an overall change of the pre–shaping profile. In contrast, an alteration of the start orientation affected the manipulation and the transport components to a similar extent. These results give further evidence that hand orientation is neither planned nor controlled independently from the other movement components. Moreover, when the grip had to match specific object properties, adjustments were mainly achieved within the first movement part. In contrast, when there were no movement constraints the final finger positions were influenced by the initial start posture of the hand. We found no evidence for a fixed spatial or temporal coupling of the grasp and the transport component in our experiments.

Introduction

During reach-to-grasp movements, 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 (Jeannerod, 1981, 1984). Maximum grip aperture (MGA) has thereby turned out to be the most prominent kinematic landmark that is sensitive to most changes in task demands like variations in object size (e.g., Jeannerod, 1981; Marteniuk, Leavitt, MacKenzie, & Athenes, 1990), object shape (e.g., Gentilucci et al., 1991; Zaal & Bootsma, 1993), and object weight (e.g., Weir, MacKenzie, Marteniuk, & Cargoe, 1991; Johansson & Westling, 1988; Gordon, Forssberg, Johansson, & Westling, 1991; for review see Smeets & Brenner, 1999). Moreover, the grip component is not only influenced by the physical dimensions of an object but also by dynamic aspects and accuracy constraints of the movement (Wing, Turton, & Fraser, 1986; Zaal & Bootsma, 1993). Although movement parameters vary depending on the requirements of the grasping task the general pre-shaping of the hand remains a highly stereotyped motor pattern.

Jeannerod (1984) was among the first to formally describe grasping behavior. He postulated that grasping consists 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 mostly reached at about two thirds of the movement duration, Jeannerod (1984) stated that both components work independently but are temporally coupled. This classical description of grasping is still rather influential and many models have been centered around the precise nature of this coupling by proposing several timing mechanisms (e.g., Bootsma & van Wieringen, 1992; Hoff & Arbib, 1993; Hu, Osu, Okada, Goodale, & Kawato, 2005). Besides these models being founded on the concept of temporal coupling of transport and grasp, there are other models that suggest that transport and grasp are spatially coupled (e.g., Haggard & Wing, 1998; Alberts, Saling, & Stelmach, 2002; Rand & Stelmach, 2005). The main idea of these models is that the distance traveled by the wrist after MGA (aperture closure distance) remains relatively invariant under different task constraints.

The assumption that there are two different visuo–motor channels working in parallel without sharing information, however, has also been challenged by perturbation studies. If the object position related to the transport component and/or the object size related to the manipulation component were perturbed at the beginning of the grasping movement, there were also changes observed in the component which was not directly affected by the perturbation (Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991; Paulignan, Jeannerod, MacKenzie,

& Marteniuk, 1991; Castiello, Bennett, & Chambers, 1998; Bennett & Castiello, 1995). Furthermore, this very influential view on grasping was also questioned by Smeets and Brenner (1999), who proposed an alternative model which assumes that the final finger position is the only controlled variable in prehension. This model, which describes the movement of the fingers using the minimum jerk approach predicts most of the experimental results in grasping accurately, without sub–dividing grasping into two components (reviewed in Smeets & Brenner, 1999).

Apart from perturbation studies which changed object size and/ or object position once the movement started, there are only a few studies which altered the grip prior to movement onset (Wallace, Weeks, & Kelso, 1990; Saling, Mescheriakov, Molokanova, Stelmach, & Berger, 1996; Timmann, Stelmach, & Bloedel, 1996a). In these studies participants had to start their grasping movements with their fingers initially stretched. Results showed that the grasp component "reorganized" itself during the first part of the movement while the transport component remained relatively unaltered (Timmann, Stelmach, & Bloedel, 1996b; Saling et al., 1996). Interestingly, the variation of the aperture size prior to movement onset resulted in considerable changes of the stereotyped pre-shaping profile. Instead of closing the fingers progressively in order to match the object size (which would result in the loss of a MGA) it was shown that in most trials participants began to close their fingers during the first phase of the wrist transport and then re-opened them prior to object grasp (Saling et al., 1996; Timmann et al., 1996a). However, in the study of Wallace et al. (1990) the paradoxical closing and reopening pattern was not observed. It was argued by Timmann et al. (1996a) that the reopening of the grip might occur only if the difference between initial opening aperture and object size is large enough.

In this study we want to investigate this issue more systematically by varying the size of the starting aperture as well as object size. So far, very little attention has been paid to the effects of varying the starting posture of the hand on grasping kinematics although in everyday life we rarely start grasping with the hand aligned to the body midline and all fingers pinched together, as done in most grasping studies. Thus, this study adds to the understanding of human grasping in more complex and natural situations.

In addition to the shaping of the hand due to object size, the fingers have to be oriented according to the orientation of the object to achieve a stable grip. A particular feature of adjusting the hand orientation to the object is that this process affects the grip as well as the transport component of the movement. It was proposed that object and hand orientations constitute a third component which integrates reaching and grasping components (Soechting & Flanders, 1993; Stelmach, Castiello, & Jeannerod, 1994; Gentilucci, Daprati, Gangitano, Saetti,

& Toni, 1996). According to the "schema theory of grasping" by Iberall and Arbib (1990) the two main parameters for planning a grasp are the finger aperture and "finger opposition axis" which have to be tuned to the dimensions of the object. The authors suggest that most hand postures can be described very well by these two parameters alone. Compared to grasping studies investigating the effects of object size and object position on grasping kinematics, there are very few studies that examine the role of object and hand orientation while grasping objects (Jeannerod & Decety, 1990; Stelmach et al., 1994; Gentilucci et al., 1996; Desmurget et al., 1996; Mamassian, 1997; Cuijpers, Smeets, & Brenner, 2004). In these studies the orientation of the target which participants had to grasp or to which participants had to adjust their fingers, was varied.

While the variation of aperture size before movement onset has previously been explored, we are not aware of any study that varied the orientation of the hand/fingers prior to movement start (although there are some studies varying the position of the hand relative to the target object, e.g. Roby-Brami, Bennis, Mokhtari, & Baraduc, 2000; Bennis & Roby-Brami, 2002). Again we would argue that starting the grasping movement with different hand and finger orientations reflects a common situation in everyday life.

The aim of this study is to examine the changes in grasping kinematics resulting from a change of the starting posture of the hand. We are especially interested in the way in which and over what time course the grip is adjusted to the object's properties. Furthermore, we want to investigate how the different components of the movement (transport and grasp) are affected and whether their temporal and/or spatial coupling persists if the initial start posture is changed. In the first experiment we varied the size of the starting aperture systematically. Participants had to grasp objects of different sizes starting with the fingers pinched together (closed aperture), slightly open, widely open, or fully stretched. In a second experiment we varied the orientation of the grip at movement beginning and participants had to grasp a cylinder which was presented at different positions. This was done because several studies have reported that the grip orientation depends on the movement direction (e.g., Paulignan, Frak, Toni, & Jeannerod, 1997; Roby-Brami et al., 2000). In the third experiment we used the same starting orientations of the grip but this time the orientation of the object to grasp was also changed such that participants had to orient their hands very precisely in order to grasp the object successfully.

Experiment 1

Methods

Participants

Ten undergraduate and graduate students of the Ludwig–Maximilans–University Munich (five male, five female; mean age = 28, SD = 5) participated in the experiment. They were paid 8 Euro per hour of participation. All participants were right–handed by self report, had normal or corrected-to-normal visual acuity, and were naive with respect to the purpose of the study.

Apparatus and stimuli

Participants sat comfortably on an adjustable chair within a lit room. A chin rest was used to maintain a constant head position throughout the experiment. They looked at a wooden board (72 x 50 cm) which was placed on the tabletop and served as presentation surface for the stimuli. Three cylindrical objects made of wood served as the target stimuli. All objects had a circular base (diameter of the small object 2.5 cm, diameter of the medium sized object 4.0 cm, and diameter of the large object 5.5 cm) and a height of 5.5 cm. Objects were always presented at the same position marked with a pin upon which each object was affixed.

Trajectories of the grasping movements were recorded using a Polhemus Liberty electromagnetic motion tracking system at a sampling rate of 240 Hz. Polhemus sensors were attached to the nails of the thumb, and the index finger of the right hand (using adhesive pastels: UHU-patafix, UHU GmbH, Bühl, Germany and medical tape). An additional sensor was attached to the back of the hand (wrist sensor).

Procedure

Participants began each trial with the index finger and thumb of the dominant right hand located at the starting position (marked by a pin). The exact placement of the fingers depended on the starting conditions which are described in the text that follows. The distance between starting position and object was about 30 cm. Between all trials participants were asked to keep their eyes closed. This allowed the experimenter to place the target object on the table without being watched by the participant. In addition, participants wore headphones through which different tones were presented: The first tone signaled them to close their eyes so that the experimenter could prepare a new trial by placing the object, the second tone signaled that the participants should open their eyes and to look at the object, after this preview period which lasted one second, a third tone indicated to them that they should start the grasping movement. In response to the third auditory signal, participants grasped the cylinder, lifted it, placed it halfway between object and starting position on the table, and moved their hand back to the starting position. After three seconds participants heard the first tone again which indicated that they should close their eyes. Subsequently, the experimenter returned the cylinder and prepared the next trial. No instructions were given as to speed of initiation and the speed of the movement.

There were four different conditions varying the size of the starting aperture. In the "pinched together" grip condition (PG–condition) participants began their movement with both fingers closed around the starting position. In the "small grip aperture" condition (SG–condition) participants closed the fingers around a disk which had the same diameter as the small object to grasp (2.5 cm) and a height of 1.0 cm. The object was attached centrally at the starting position. In the "large grip aperture" condition (LG–condition) participants had to grasp a disk with the same diameter as the large object (5.5 cm and 1.0 cm in height) with index finger and thumb before each trial. Finally, in the fourth condition, participants had to stretch their fingers such that the distance between index and thumb was maximal ("fully stretched" grip condition (FG–condition)). While the hand was fully stretched the starting position was located halfway between index and thumb in the interdigital space.

In all conditions participants were allowed 3 s to execute the movement. If this time limit was exceeded, the trial was classified as an error and repeated later in the experiment at a random moment. The different starting conditions were presented in blocks of 30 trials (10 trials per object size) with three practice trials preceding each condition. The order of blocks was counterbalanced across participants and the sequence of presentation within each condition was in pseudo random order.

Data Processing

The finger trajectories were filtered off-line using a second-order Butterworth Filter that employed a low-pass cut–off frequency of 15 Hz. Movement onset was defined by a velocity criterion. The first frame in which the wrist exceeded a velocity threshold of 0.1 m/s was taken as movement onset. Reaction time (RT) was defined as the time between the auditory signal and movement onset. The first frame in which the velocity of the wrist dropped below a threshold of 0.1 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, the aperture profile (3D distance between the two sensors on index finger and thumb) was determined. Since it was proposed that starting a grasping movement with open fingers leads to a closing and reopening pattern in the aperture profile, we searched for local minima and local maxima in the aperture profiles (Saling et al., 1996; Timmann et al., 1996a). Therefore, we differentiated the aperture profile for each participant and each trial until the object was touched. Whenever there was a change in the algebraic sign from minus to plus in the velocity trace, a local minimum was detected indicating a ”dip” in the aperture profile. Correspondingly, a subsequent change in the algebraic sign from plus to minus indicated a second maximum. The last maximum of this analysis was defined as maximum grip aperture (MGA) for all conditions. When there was only a single peak in the aperture profile, this peak was taken as MGA.

To characterize the transport component of the grasping movement we calculated the midpoint between index and thumb. We determined the amplitude of peak velocity (APV), time to peak velocity (TPV), the amplitude of peak deceleration (APD) and the time to peak deceleration (TPD) from this measure by differentiation of the position signal. Movement trajectories were quantified after time normalization of the data. The mean and the standard deviations of the mean X and Y positions of each sensor were calculated for each of the 100 normalized frames.

The coupling of the grasp and the transport component under different start aperture conditions was examined using a temporal and a spatial measure: To determine the occurrence of MGA temporally, the normalized aperture opening time expressed as percentage of MT, was calculated. Secondly, as a more accurate measure we correlated the relative time to MGA with the relative TPD of the wrist. For a spatial measure, we calculated the distance traveled until MGA occurred and the distance traveled from MGA to the touch of the object (c.f. Rand, Squire, & Stelmach, 2006). These distances were calculated as the cumulative resultant trajectory lengths (in x and y) between two positions of the thumb sensor. We decided to use the thumb sensor and not the wrist sensor to compute trajectory length since it was argued by Haggard and Wing (1997) that the motor system is more concerned with thumb position than with wrist position during hand transport.

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 $\alpha = .05$ was used for the statistical analyses.

Results

Kinematics of the grip component

MGA and aperture profiles: We examined the changes in the aperture profile due to different sizes of the starting aperture of the hand. The most prominent landmark of the kinematic profile is therefore the MGA. Figure 1 shows the mean size of the start aperture in different conditions and the corresponding MGAs. The MGA was of similar size in all conditions and, as expected, was influenced by object size. That the MGA was overall a bit larger in the FG–conditions can be explained by the fact that when there was no second (late) peak in the aperture profile, the MGA was determined as the first peak which occurred shortly after movement onset. (Note, that in the trials in which MGA occurred simultaneously with the movement onset, no MGA was determined.)

Insert Figure 1 about here

As discussed above, studies introducing an altered aperture at movement beginning reported a pattern of aperture closing and reopening instead of a smooth closing of the fingers (e.g., Saling et al., 1996; Timmann et al., 1996a). Here we examined the occurrence of a local minimum ("dips" which indicates an initial aperture closing) in the aperture profile in a systematical way (see also Hesse & Franz, 2008). Figure 2 shows the percentage of movements with a "dip" averaged over all participants for the different start aperture conditions. The repeated–measures ANOVA revealed no effect of object size, $F(2, 18) = 1.1, p = 0.34$, but a significant effect of start aperture $F(3, 27) = 13.2, p = 0.001$. Post–hoc tests indicate that there were significantly fewer "dips" when participants began their grasp with all fingers pinched together compared to all other conditions (all $p < .008$). No interaction effect was found ($p = .17$). In Figure 3 representative single subject trials are depicted for the different conditions. The finding that there are approximately 20–30% of "dips" in the pinched together conditions is consistent with our recent results on the occurrence of double–peaks during normal grasping (Hesse & Franz, 2008), since the occurence of a secondary peak in the aperture profile always corresponds with the occurrence of a local minimum.

Insert Figure 2 about here

Insert Figure 3 about here

To investigate the changes in the grip over time in further detail we also calculated the mean aperture profiles over all participants. For this purpose, we time–normalized each movement from its onset until the touch of the object, and calculated the size of the aperture every 5% of the movement time. As seen in Figure 4 the aperture profile in all four conditions gets similar shortly before MGA or before the second peak is reached. Thus, the closing–phase remains alike over all conditions. This implies that the variation of the start aperture size only affects the first half of the movement. The mean trajectories of the fingers and the wrist for the different conditions are depicted in Figure 5.

Insert Figure 4 about here

Insert Figure 5 about here

Kinematics of the transport component

RT and MT: RT and MT were neither influenced by the size of the starting aperture nor by the changes of object size (all $p > .34$). On average it took participants $293ms \pm 16ms$ to initiate and $699ms \pm 27ms$ to complete the grasping movement.

Velocity and deceleration: It was often observed that wrist movements in a standard grasping task have a single peak and a bell–shaped velocity profile. Thus, they can be well characterized by measuring the amplitude and the (relative) timing of peak velocity and peak deceleration (e.g., Paulignan, MacKenzie, et al., 1991; Paulignan, Jeannerod, et al., 1991). Figure 6 shows the mean values of all wrist parameters. A 4 (start aperture size) x 3 (object size) repeated measures ANOVA applied on the data revealed that the object size as well as the start aperture size had no effect on any of the wrist parameters measured (see Table 1).

Insert Table 1 about here

Insert Figure 6 about here

Coupling

Timmann et al. (1996a) reported that in 60% of all trials in which participants started their grasping movement with the fingers apart the wrist velocity profile also showed an inflection (additional peak). They supposed that this second peak might indicate that transport and grasp component are planned together. We looked for an additional inflection of the wrist velocity profile in the same way as for the aperture profile, by searching for local maxima. Overall, we found fewer secondary peaks in the wrist velocity profile than Timmann et al. (1996a): 11.4% ± 3.9% in the PG–condition (which can be considered as baseline), 15.3% ± 4.0% in the SG–condition, 15.0% ± 5.3% in the LG–condition, and 28.2% ± 8.6% in the FG condition. Therefore, data indicated only a tendency for slightly more additional peaks in the FG–condition, $F(3, 27) = 3.2, p = .08$.

Spatial and temporal coupling: As discussed in the introduction there are different theories suggesting a spatial (e.g., Haggard & Wing, 1998; Alberts et al., 2002; Rand & Stelmach, 2005) versus a temporal coupling (e.g., Jeannerod, 1984; Paulignan, MacKenzie, et al., 1991; Hoff & Arbib, 1993) of the grasp and transport components. In this study we wanted to test if there is a fixed spatial or temporal coupling if the size of the start aperture is varied. In Figure 6f, the distances traveled by the thumb from movement onset to the occurrence of MGA and from MGA to the touch of the object are shown for the different start aperture conditions. It was proposed that the distance which has to be covered by the hand after MGA, remains relatively stable under different movement conditions (e.g., Alberts et al., 2002; Rand & Stelmach, 2005; Rand et al., 2006). Figure 6f shows that the distance traveled after MGA until the touch of the object is much longer in the FG–conditions ($11.0cm \pm 2.5cm$), whereas it was of similar length in all other conditions, PG–conditions ($3.7cm \pm 0.5cm$), SG–conditions ($3.1cm \pm 0.6cm$) and LG–conditions ($4.0cm \pm 0.8cm$). The larger distances in the FG–conditions result most likely from the trials in which participants show an early first peak and no second late peak in the aperture profile. Additionally, we found a significant effect of object size on the aperture closure distance, $F(2, 18) = 9.3, p = .004$. Post–hoc tests indicate, that participants start to close their fingers earlier when grasping smaller objects ($all p < .04$).

A rough measure of the temporal coupling of the grasp and the transport is the occurrence of MGA within MT, which was supposed to be relatively fixed (Jeannerod, 1984; for review see, Smeets & Brenner, 1999). Therefore, we further examined the effect of the different start aperture sizes on the aperture opening time expressed as percentage of MT. Figure 6e shows that the MGA in the FG–conditions (57% ± 7%) was reached earlier in MT than in all the other conditions (79% ± 2% in the PG–conditions, 81% ± 2% in the SG–conditions, and 77% ± 2% in the LG–conditions). Furthermore, we observed a significant effect of object size which indicates that the MGA occurres later in MT when the object size increases, $F(2, 18) = 15.4, p < .001$. The interaction between object size and size of the start aperture also became significant, $F(6, 54) = 2.7, p = .05$. Since many studies have shown that the relative timing of MGA varies with task demands, one could argue that the occurrence of MGA within the MT might be a too simplistic measure to detect the temporal coordination of grip and transport. Hence, we also correlated the relative time to MGA with the relative TPD of the transport component, which is supposed to be a more robust measure of temporal coupling. However, none of these correlations were found to be significant. This implies that both components were not strictly temporally coupled.

Discussion

In this experiment, we disturbed the well known biphasic grip pattern consisting of an opening of the fingers until the MGA, and the subsequent closing until the object is touched, by varying the size of the aperture openings before movement onset. Our findings confirm the observation that the grip formation is altered during the first half of the movement whereas the second half of the movement remains relatively unchanged. The grip formation, when beginning the movement with the fingers apart, is mainly characterized by an initial closure of the grip resulting in a dip in the aperture profile (Timmann et al., 1996a; Saling et al., 1996). By using different start aperture sizes as well as different object sizes, we could show that the initial closing of the aperture does not only occur when the fingers are fully extended but equally often when the aperture is only slightly open at movement onset. We found no evidence for the proposition that the closing and re–opening of the aperture only occurs if the difference between the aperture size and the object size is very large, as suggested by Timmann et al. (1996a). Additionally, in the SG–condition participants had to open their fingers wider in order to grasp the object successfully whereas in the FG–conditions the fingers had to close only. Despite this difference, the closing and reopening pattern was found in both conditions. Interestingly, it was already pointed out by Smeets and Brenner (2002) that neither their model on digit control (Smeets & Brenner, 1999) nor the more complex posture model of Rosenbaum, Meulenbroek, Vaughan, and Jansen (2001) can correctly predict the alterations of the grip profile due to different start aperture sizes.

However, there is another possible explanation for the occurrence of the first peak and the subsequent closing (”dip”) in the aperture profile in the SG and LG–conditions (cf. Figure 3). In these conditions, participants hold a real object (the start disc) between their fingers at movement onset. Thus, the first part of the aperture profile could also represent the release of the start object. In that case the change in the profile would indicate the superposition of two sub–movements: releasing the first object and grasping the second object. In a pilot study we checked for this simple explanation: five participants (which also participated in Experiment 1) repeated the SG and LG–conditions without holding a real object between their fingers. The size of the start aperture was marked on the presentation board and corresponded to the size of the starting discs used in the SG–conditions and LG–conditions, respectively. Using these conditions we still found an increased percentage of local minima compared to the PG–conditions: $51\% \pm 7\%$ for the SG–conditions and $67\% \pm 10\%$ for the LG–condtions. Overall, we observed that the initial closing persisted while the initial peak (prior to the dip) became less pronounced when no object was held prior to movement onset. The fact that there is an initial closing of the aperture is also consistent with our observation of the aperture closing and re–opening in the FG–conditions since in these conditions no object was held between the fingers.

Concerning the transport component of the grasping movement, we were able to replicate the finding that the variations of the start aperture did not affect the main kinematic landmarks (Timmann et al., 1996a; Saling et al., 1996). The grip was executed equally fast in all conditions. This finding suggests that all start apertures are treated as equally likely by the motor system. In other words, no additional on–line correction is required when participants start grasping with the fingers apart. Furthermore, we found no evidence for an additional inflection in the wrist velocity profile at the time the fingers start to reopen as observed by Timmann et al. (1996a). However, Timmann et al. (1996a) proposed themselves that the additional inflection in the wrist velocity profile found in their data might be due to the slowness of the movement resulting in discontinuities in the wrist velocity profile (see also Milner, 1992).

Finally, we questioned how the occurrence of MGA was affected temporally and spatially by a change of start aperture size. The data revealed a surprisingly consistent temporal and spatial occurrence of the last aperture peak in the PG, SG and LG–conditions. Only when the grip was started with a fully stretched hand the MGA was reached earlier and farther away from the target. This finding is because of that in some trials participants close their grip continuously after a short closing and re–opening in the beginning of the movement. However, aperture closure distance as well as the relative timing of the MGA were affected by the size of the target object. In summary, these findings neither support a fixed temporal linkage between transport and grasp components nor do they support a mere spatial coordination. In fact, our results suggest that the motor system programs and executes an effective movement which takes both, the initial aperture size and the size of the target object into account.

So far, our study replicates and extends the findings of what happens to the grip pattern when the size of the aperture is varied prior to movement onset. In the second experiment we were interested in how the grasping movement is altered if the orientation of the aperture/hand is changed prior to movement onset. This is especially interesting since it was proposed that the orientation of the hand plays a special role affecting transport as well as grasp component of the movement. Thus, we would hypothesize that altering the starting orientation of the aperture also affects the transport component of the grasping movement.

Experiment 2

In this experiment we investigated the effect of different start aperture orientations on grasping. Again we were interested in how the start posture of the hand is taken into account during movement execution. In contrast to Experiment 1, we hypothesized that the orientation of the grip affects both, the grip and the transport component of the movement.

Methods

Participants

Ten undergraduate and graduate students of the Ludwig–Maximilans–University Munich (four men, six women; mean age = 25, SD = 5) participated in the experiment. They were paid 8 Euro per hour for participation. All participants were right–handed by self report, had normal or corrected-to-normal visual acuity and were naive with respect to the purpose of the study.

Apparatus and stimuli

The apparatus and the general procedure were identical to Experiment 1. In this study, only one cylinder with a diameter of 40 mm was used as target object (same object as the medium–sized cylinder in Experiment 1). The cylinder could be presented at three different positions on the working surface: (a) middle: straight on from the starting position, (b) left: 45° to the left away from the starting position, (c) right: 45° to the right from the starting position (cf. Figure 7A). In all three conditions, the distance between the starting position and the object was 30 cm. Participants began each trial with their fingers closed around a wooden starting–cube (2x2x2 cm) which was placed in the middle of the working surface 12 cm away from the edge of the table. Depending on the condition, the starting–cube was oriented vertically (parallel to the sagittal plane), or the starting–cube was rotated by 45°. Participants were asked to place their fingers in four different orientations on the starting–cube (Figure 7B). The different starting conditions were presented in blocks of 30 trials (10 trials per object position) with three 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.

Participants were asked to grasp the cylinder with a precision grip using index finger and thumb to which the Polhemus sensors were attached. A third sensor was attached to the back of the hand.

Insert Figure 7 about here

Data Processing

Since the task primarily involved horizontal movements and only the horizontal orientation of the starting grip aperture was manipulated, we only analyzed the horizontal orientation of the grip (azimuth). 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. The MGA was defined as the maximum distance between the index and the thumb in 3D during MT. All other dependent variables RT, MT and the parameters of the transport component were determined identical to Experiment 1.

Results

Kinematics of the grip component

Grip rotation: Our main interest lay in the alteration of the grip orientation over time. For that reason, we calculated the rotation of the grip every 5% of the movement time, as done for the aperture profiles in Experiment 1. The changes of the grip rotation over time and for the different object positions are shown in Figure 8. Visual inspection of this figure shows that the grip is mainly rotated in the first part of the movement. The final grip orientation appears to be reached at roughly 70% of MT (which corresponds approximately to the occurrence of MGA). Furthermore, we performed a repeated–measures ANOVA at 3 different moments in time (grip rotation at: (1) movement onset, (2) moment of MGA, and (3) touch of the object). At the movement onset the grip rotation was, as expected, strongly influenced by the start orientation, $F(3, 27) = 693.6, p < 0.001$, but not by the position of the object, $F(2, 18) = 3.1, p = .11$. On average, the start orientation of the grip was $-34° \pm 1.8°$ for the -45°condition, $-1° \pm 1.2°$ for the sagittal start orientation, $38° \pm 1.1°$ for the 45°start orientation and $70° \pm 2.0°$ for the lateral start orientation.

Orientation of the grip at its maximum did depend on the start orientation, $F(3, 27) = 19.4, p < .001$ as well as on the position of the object, $F(2, 18) = 112, 4, p < .001$. These effects persisted for the moment the target object was touched, $F(3, 27) = 14.1, p = .001$, for the start orientation and $F(2, 18) = 127.7, p < .001$, for the object position. None of the interactions became significant (all $p > .17$). Thus, the grip orientation at the end of the movement was still biased to the orientation of the fingers taken before movement onset. The result that the orientation of the fingers is influenced by the position of the object is in line with the findings of other studies (e.g., Gentilucci et al., 1996; Roby-Brami et al., 2000; Bennis & Roby-Brami, 2002).

Insert Figure 8 about here

MGA: In order to investigate whether there is an effect of aperture orientation and object position on MGA while grasping the cylinder, a 4 (aperture start orientation) x 3 (object position) repeated-measures ANOVA was carried out. The ANOVA only revealed a main effect of start orientation, $F(3, 27) = 5.9, p = .006$. Participants opened their hand wider when they started their movement with the left and the sagittal start orientation compared to the right and the lateral start orientation of the aperture. No main effect of object position ($p = .26$) and no interaction ($p = .21$) was found.

Kinematics of the transport component

RT and MT: To analyze the effects of start aperture orientation and object position on RT and MT a 4 (aperture start orientation) x 3 (object position) repeated-measures ANOVA was applied on the data. No effects of the experimental variations were found on RT (all $p > .10$). However, MT was significantly affected by both, orientation of the start aperture, $F(3, 27) = 10.4, p = .002$ and object position, $F(2, 18) = 51.3, p < .001$. There was no interaction ($p = .06$). Post–hoc tests revealed that MT increases the more the start orientation was rotated clockwise being fastest in the -45° condition and slowest in the condition in which the grip was oriented laterally. Furthermore, MT was shortest when the object was located at the right side of the working surface ($613ms \pm 19ms$), slightly longer when it was presented in the middle position ($668ms \pm 18ms$), and longest when it was presented at the left location ($725ms \pm 18ms$).

Velocity and deceleration: As in Experiment 1, we characterized the transport component by the amplitude and timing of peak velocity and peak deceleration. In Figure 9a-d the mean values of all these parameters are shown. A 4 (start aperture size) x 3 (object size) repeated measures ANOVA applied on the data revealed that object position had strong effects on all wrist parameters measured (see Table 1). Further, the transport component was also very susceptible to the changes of start aperture orientation. Thus, the object position as well as the start orientation of the grip taken before movement onset influenced the kinematic parameters of the transport component.

Insert Figure 9 about here

Coupling

The coupling of grasp and transport component was again measured spatially and temporally. The mean opening and closing distances for the different conditions are shown in Figure 9f. A 4 (start orientation) x 3 (object position) repeated–measures ANOVA revealed no effect of the start orientation, $F(3,27) = 0.3, p = .68$. However, the aperture closing distance was affected by the object position, $F(2,18) = 5.3, p = .04$. The hand started to close farther away from the object when it was presented at the left position ($6.9cm \pm 1.7cm$), a bit closer to the object when it was presented in the mid position ($6.0cm \pm 1.4cm$), and closest to the object when it was presented to the right ($5.0cm \pm 1.0cm$). We also observed a significant interaction, $F(6,54) = 3.6, p = .02$, which suggests that changes in the start orientation affect the spatial occurrence of MGA differently depending on the object's position. With respect to the relative occurrence of MGA, during MT no effect of start orientation ($p = .23$) and object position ($p = .75$) was found. On average the MGA was reached at about $70\% \pm 4\%$ of MT (see Figure 9e). As in Experiment 1, we examined the temporal coupling of the transport and the grasp components further by correlating the relative time to MGA with the relative time to TPD of the transport component. When the grip was oriented to the right or the left prior to movement onset, none of these correlations were found to be significant (all $p > .07$). In the lateral condition the correlation became only significant when the right object was grasped ($r = .79$ and $p = .007$, all other $p > .20$) and in the sagittal condition when the object was either presented in the middle or to the right ($r = .72$ and $p = .02$ and $r = .83$ and $p = .003$). To conclude, we observed a significant correlation only in three out of the twelve conditions presented.

Discussion

In this experiment we investigated the effects of changing the hand orientation prior to movement onset in grasping. We replicated the finding that the orientation of the grip axis was strongly affected by the position of the object and movement direction of the hand respectively (Gentilucci et al., 1996; Paulignan et al., 1997; Roby-Brami et al., 2000). More interesting was, however, that the grip orientation, even at the end of the movement, depended on the start orientation of the aperture. Since the target object was a cylinder, it had no specific opposition axis which had to be chosen in order to achieve a stable grasp. The occurrence of a bias in the direction to the initial orientation suggests that the motor system takes the information about the initial posture into account while planning and executing the movement. Therefore, the experiment provides evidence that the initial hand orientation influences the selection of the grasp axis when grasping an object with a neutral orientation.

Additionally, we found an effect of the start orientation on MGA which is regarded as the main kinematic landmark of the grasp component. It should, however, be noted that the variations of the grip orientation on which we placed our emphasis always implied a rotation of the wrist. In case of the left and the sagittal grip orientation a flexion of the wrist is required whereas the right and the lateral grip orientation are linked to an extension of the wrist at the start position. Thus, we cannot clearly separate which effects are due to the orientation of the aperture and which are due to the different postures of the wrist prior to movement onset.

Furthermore, when holding the starting–cube in the different starting conditions not only the flexion and extension of the wrist changes, but also its position relative to the target object. Holding the starting–cube in the -45°orientation between index and thumb requires a location of the wrist above the fingers in the direction of the working surface (see also Figure 7B). A clockwise rotation of the aperture also demands a clockwise rotation of the wrist rotating away from the working surface in direction to the participant's body. This means the more the grip is rotated clockwise the longer the distance which the wrist has to cover to reach the target object becomes. (Note that this was also the reason why we decided to measure the transport component as the midpoint between index and thumb.) Thus, the finding that MT increases the more the start orientation of the hand is rotated clockwise might be due to the fact that movement distance of the wrist increases. The main effect of object position on MT suggesting that movements in the ipsilateral space are accomplished faster than movements in the contralateral space. Moreover, transport kinematics calculated from the midpoint of the fingers were also influenced by start orientation and object position.

Thus, in contrast to the changes of aperture size prior to movement onset (Experiment 1), the changes of initial hand orientation had considerable effects on the transport kinematics of the grasping movement.

In summary, our results show how interrelated the different components of grasping are. Varying the start orientation of the hand affected most of the parameters that characterize grasping. As discussed above, the alteration and the adjustment of the grip orientation also implies changes in the orientation of the wrist. Thus, we would argue that the orientation of the hand does not seem to constitute a third independent visuomotor channel besides transport and grasp as proposed by some theories (e.g., Arbib, 1981; Laquaniti & Soechting, 1982; Stelmach et al., 1994; Fan, He, & Helms Tillery, 2006). Instead, our results support the assumption that the orientations of hand and wrist integrate the distal transport component and the proximal grasp component (e.g., Desmurget et al., 1996; Gentilucci et al., 1996).

So far we have shown that a change of aperture size (Experiment 1) and a change of aperture orientation (Experiment 2) prior to movement onset alters the execution of the grasping movement. A fundamental difference between Experiments 1 and 2 is that in case of a change in aperture size, the grasp was forced to completely adjust to the size of the target object in order to grasp it successfully. In contrast, in Experiment 2, the grip orientation did not have to be adjusted to a specific object orientation resulting in different grasp orientation in the end of the movement. In a third experiment we explored the effects of different start orientations when a precise adjustment of the grasp axis is required.

Experiment 3

In Experiment 2 we observed that the start orientation taken before movement onset still influenced the grip orientation at the moment the target object was touched. Since the target object was a cylinder, the chosen grip orientation did not have to be very exact. In Experiment 3 we investigated the adaptation of grip orientation to a target object which required a very precise alignment of the grip axis.

Methods

Participants

Eight undergraduate and graduate students of the Ludwig–Maximilans–University Munich (three men, five women; mean age = 26, SD = 5) participated in the experiment. They were paid 8 Euro per hour for participation. All participants were right–handed by self report, had normal or corrected-to-normal visual acuity and were naive with respect to the purpose of the study.

Apparatus and stimuli

The apparatus and the general procedure were identical to Experiment 1 and 2. In this experiment, the target object was a cylinder with a diameter of 10 mm and a height of 40 mm. In contrast to Experiment 1 and 2 the cylinder was presented in a lying position meaning that it had to be grasped along the 40 mm axis (same diameter as the object in Experiment 2). Thus, the narrow ends of the cylinder represented the contact surfaces of the fingers (see inset of Figure 7A). The cylinder was presented in three different orientations: (a) sagittal: 90°, (b) left: -45° to the left, (c) right: 45° to the right. The object was always presented at the same location as the central target in Experiment 2 (Figure 7A). Participants started with the same starting orientations as in Experiment 2 (Figure 7 B). The different starting conditions were presented in blocks of 30 trials (10 trials per object orientation) with three 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.

Participants were asked to grasp the cylinder with precision grip using index finger and thumb to which the Polhemus sensors were attached. A third sensor was attached to the back of the hand. All data analysis were identical to Experiment 1 and 2.

Results

Kinematics of the grip component

Grip rotation: All analyses of the aperture were performed equivalent to Experiment 2. Figure 10 shows the mean aperture orientation profiles for all start orientations and object orientations. In contrast to Experiment 2, the grip orientation was the same in the end of the movement no matter what the start orientation of the grip was. This was also confirmed statistically. We calculated a repeated–measures ANOVA at three different moments at time. At movement onset the grip orientation was affected by the start orientation of the grip, $F(3, 21) = 387.4, p < .001$, but also by object orientation, $F(2, 14) = 9.1, p = .009$. The fact that object orientation affected grip orientation even at movement onset might most likely be due to the determination of movement onset which was defined by wrist velocity. The difference between the three orientations was, however, only about 1°. At MGA the grip orientation became much stronger affected by the object orientation, $F(2,14) = 100.9, p < .001$, and was still affected by the start orientation of the aperture, $F(3,21) = 6.7, p = .01$. At the touch of the object, the grip orientation was no longer influenced by the start orientation, $F(3,21) = 0.8, p = .46$, but, as expected it was influenced by the orientation of the object to grasp, $F(2,14) = 1291.1, p < .001$. For the left oriented object the final grip orientation was $-32° \pm 2.6°$, for the vertical cylinder it was $7° \pm 1.5°$, and for the right oriented cylinder grip the orientation was about $43° \pm 0,9°$. None of the interactions became significant (all $p = .31$).

Insert Figure 10 about here

MGA: In contrast to Experiment 2, the repeated–measures ANOVA on MGA revealed no effect of start orientation ($p = .86$). However, object orientation influenced the size of MGA significantly, $F(2,14) = 15.2, p = .003$. Post–hoc tests showed that the size of MGA was smallest for the left oriented object ($8.8cm \pm 0.2cm$), larger for the vertical object ($9.6cm \pm 0.4cm$), and largest for the right oriented object ($10.1cm \pm 0.5cm$). There was no interaction observed ($p = .37$).

Kinematics of the transport component

RT and MT: As in Experiment 1 and 2, RT was not affected by any of the experimental variations (all $p > .32$). Regarding the MT we found an effect of start orientation, $F(3,21) = 22.2, p < .001$, replicating the finding of Experiment 2. Again, MT increased the more the start aperture was rotated in the clockwise direction being shortest for the left orientation and longest for the lateral orientation. There was also a significant effect of object orientation on MT, $F(2,14) = 70.8, p < .001$. MT was longest when the object was oriented to the left ($745ms \pm 13ms$), shorter when the object was oriented vertically ($682ms \pm 12ms$), and shortest when the object was oriented rightward ($654ms \pm 8ms$). There was no interaction ($p = .21$).

Velocity and deceleration: The transport component was again characterized by the amplitude and timing of peak wrist velocity and peak wrist deceleration (see Figure 11a-d). Similarly to Experiment 2, the start aperture orientation affected the transport component considerably (Table 1). The orientation of the object influenced the timing of peak velocity and peak deceleration but not the amplitudes. The effects of start aperture orientation and object orientation did not interact. In sum, these findings replicate the results of Experiment 2 suggesting that the start orientation of the hand influences the transport component of the grasping movement.

Insert Figure 11 about here

Coupling

As in Experiment 1 and 2, the coupling of grasp and transport component was analyzed spatially and temporally. The mean opening and closing distances for the different conditions are shown in Figure 11f. A 4 (start orientation) x 3 (object orientation) repeated–measures ANOVA applied on the data showed, as in Experiment 2, no main effect of start orientation on aperture–closing distance ($p = .37$). However, aperture–closing distance was significantly affected by the object's orientation, $F(2, 14) = 9.2, p = .02$. Post–hoc tests revealed that the maximal aperture opening was reached farther away from the target object if it was oriented leftward. There was also a significant interaction found here, $F(6, 42) = 3.9, p = .02$. Therefore again, the aperture closing distance did not reveal itself to be an invariant parameter in grasping.

Regarding the relative occurrence of MGA during MT, no effect of start orientation ($p = .47$) was observed (Figure 11e). This finding is consistent with our results of Experiment 2. The orientation of the object, however, influenced the relative timing of MGA significantly, $F(2, 14) = 11.4, p = .003$. On average the MGA occurred at 61% ± 5% of MT for the left oriented object, at 74% ± 4% of MT for the vertically oriented object, and at 74% ± 5% of MT for the right oriented object. There was also a significant interaction between the start orientation and the object orientation, $F(6, 42) = 3.6, p = .03$. Thus, the relative timing of MGA as well as its spatial position differed when the orientation of the object was changed, and the magnitude of this effect depended on the start orientation of the hand. As in Experiment 1 we examined the temporal coupling of transport and grasp further by correlating the relative time to MGA with the relative time to TPD of the transport component. None of these correlation were found to be significant (all $p > .28$).

Discussion

In this experiment we investigated the effect of different start orientations of the hand on grasping kinematics when the finger opposition axis must be aligned very accurately to the object opposition axis. The adjustments of the grip orientation to the object's orientation started at movement onset and were accomplished after approximately 60% to 70% of the movement duration.

Furthermore, the grasp as well as the transport component were significantly affected by the orientation of the object to grasp. The finding that object orientation not only influences the rotation of the hand but also its opening and transport, is in line with the results of Mamassian (1997). We already discussed that the orientation of the hand prior to movement onset influences the position of the hand which could explain the effects of start orientation on MT. The same argument holds for the orientation of the object. In addition, the wrist has to be flexed when the right oriented object had to be grasped and extended when the left oriented object had to be grasped. Depending on the start orientation of the hand, this flexion and extension had to be integrated into the movement plan. Since we found no significant interaction of start orientation and object orientation on MT, the rotation of the wrist is achieved without any additional time costs, which is in accordance with the findings of Stelmach et al. (1994). However, the velocity characteristics of the transport component which were determined independent of the movement distance were also influenced by start aperture orientation as well as object orientation showing that transport parameters are susceptible to these variations.

Moreover, we observed neither a fixed temporal nor a fixed spatial coupling between grasping and transport component for the given task. This suggests that the repeatedly observed temporal coupling might be due to the non–complexity of the grasping task used (object that was placed in front of the participants who began their movement with the fingers pinched together). Here we found that when the task becomes more difficult, involving a rotation of the fingers and the hand, the coupling between transport and grasp is altered. The finding that the aperture closing distance varies with object orientation contradicts the results of Rand and Stelmach (2005). They showed that aperture closure is generally initiated at roughly the same distance for different target orientations. Based on their data they concluded that grasping is coordinated based on spatial rather than on temporal information. However, another study by the same group proposed that aperture closing distance varied with movement speed thereby questioning the assumption that this parameter remains constant when the task requirements change.

In summary, the various effects of the start orientation and the object orientation on transport and grasp kinematics, suggest that the orientation of the hand is very closely related to both components and does not constitute a third independent visuomotor channel. If the hand orientation comes into play during grasping, the changes in movement kinematics and the interrelations appear to become much more complex. Paulignan et al. (1997) have also stated in a study that the use of a broader range of conditions changes the view on visuomotor transformations. In other words using more complex conditions reveals the interdependence of the underlying mechanisms for matching object position, orientation and size in grasping. This notion is further supported by our results.

General Discussion

In this study, we investigated the way in which different hand postures taken prior to the movement onset alter the kinematics of the grasping movement. We hypothesized that the assumption that grasping is a relatively stereotyped movement pattern, might be due to the fact that the movements were primarily investigated using a standard grasping task. The classical experimental grasping task requires that participants begin their grasping movement with all fingers pinched together at a given starting location which is often aligned to the body midline or slightly to the right of the participants' body (if right handers are examined).

From these studies it is well known that: (a) the size of the object strongly influences the grasp component such as the MGA and its timing (e.g., Jeannerod, 1984; Marteniuk et al., 1990; Bootsma, Marteniuk, MacKenzie, & Zaal, 1994; Smeets & Brenner, 1999), (b) the position and the distance of the target object primarily affect the transport component of the movement such as MT and PV (e.g., Jeannerod, 1984; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Jakobson & Goodale, 1991), and (c) that the orientation of the object changes the kinematics of both components, transport and grasp (e.g., Stelmach et al., 1994; Desmurget et al., 1996; Gentilucci et al., 1996; Mamassian, 1997), hence hand orientation was sometimes considered to constitute a third (independent) component of the grasping movement (e.g., Arbib, 1981; Fan et al., 2006). However, it is still a matter of debate whether the components of transport and grasp are independent of each other. Whereas studies using simple grasping tasks are in favor of two (or three) independent visuomotor channels which are merely temporally coupled (Jeannerod, 1984; Arbib, 1981), studies using more complex grasping tasks give evidence for the interdependence of all components (Paulignan et al., 1997; Desmurget et al., 1996). In addition, there are studies which are in favor of a spatial coupling of transport and grasp component (e.g., Haggard & Wing, 1998; Alberts et al., 2002; Rand & Stelmach, 2005).

In Experiment 1 in which only the size of the start aperture was changed prior to movement onset we replicated the finding of a substantial alteration of the grasp component while the transport component remains relatively unaffected (Saling et al., 1996; Timmann et al., 1996a). Our experiment extends earlier studies insofar as we included more conditions varying the size of the aperture at movement onset. Therefore, we could show that the closing and reopening of the aperture occurs not only when the fingers are fully stretched but also if fingers were slightly open and had to open further to grasp the object successfully.

Although the distinct peak at movement onset may result in part from the release of the starting disc, the tendency to close the fingers first before starting the final grip is also preserved when there is no object to be grasped prior to movement onset.

In Experiment 2 and 3 in which we varied the start orientation of the aperture prior to movement onset, we found considerable changes in both components, manipulation and transport. While the altered start aperture in Experiment 1 selectively influenced the grasp component leaving the overall position of the hand unaffected, the variation of the start orientation was not only associated with a change of the finger position in space, but also with a change of the hand position and the rotation of the wrist. Since the selection of the finger opposition axis determines the position of the hand in work space, it seems very unlikely that the hand orientation constitutes a third independent movement component besides reach and grasp. To accomplish the task successfully all joints involved in the process of adjusting the hand orientation to the object orientation must share information during movement planning, execution and control. Thus, if the movement becomes increasingly complex the sub–processes of grasping must be integrated so that the movement is controlled holistically. It was suggested by Desmurget et al. (1996) that some ”higher–order control system” might take over the integration of hand transport and hand orientation in such an event.

Regarding the coupling of transport and grasp, our results neither support a fixed temporal nor a fixed spatial relationship of both components. It has repeatedly been shown that the relative timing of MGA varies not only with object size (e.g., Marteniuk et al., 1990) but is also related to movement difficulty, such as accuracy and object visibility (for review, Smeets & Brenner, 1999). Here we could show that the timing of MGA within MT also depends on the start posture of the hand and the related task demands (as indicated by significant interactions in Experiment 1 and 3). Besides, it was proposed that the temporal linkage between grasp and transport consists in a high correlation between relative time to MGA and the relative timing of peak deceleration of the wrist (Jeannerod, 1984). However, in our data we found very few correlations between these two variables (only in some of the conditions of Experiment 2) which suggests that this relationship may change with task demands. Similarly, the distance at which the hand began to close relative to the target object varied with the task demands being in contrast with the models which predict a fixed spatial relationship (Alberts et al., 2002; Rand & Stelmach, 2005). Thus, none of the models in grasping based on an invariant temporal or spatial coupling of both components can account for our results. In contrast to these models, Marteniuk et al. (1990) suggested that transport and grasp might be primarily functionally linked, i.e. that their exact temporal and/or spatial relationship depends on the task requirements.

According to this proposition the transport and the grasp components are coordinated such that a given task can be achieved efficiently and successfully. This proposition best suits our observations.

In conclusion, our experiments show that grasping kinematics change considerably if the start posture of the hand is varied. The more complex the alteration of the start posture, the more the kinematic parameters involved were affected by it. If it is necessary to adopt a certain end–posture to grasp an object successfully, the grip is mainly modulated during the first half of the movement. If there was, however, no need to adjust the hand to specific object properties (Experiment 2) then the final posture of the hand at lift–off of the object was still affected by the start posture adopted. This finding suggests that the motor system plans an economical and efficient movement taking the actual start posture of the hand into account.

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Acknowledgement

This study was supported by of the Cluster of Excellence "Cognition for Technical Systems" (Project 301) and by 7th Framework Programme of the European Community (project "GRASP", ICT-215821). We thank Devika Narain for help with the data collection.

Figure Legends

Figure 1: Experiment 1: The effect of the start aperture size and the object size on MGA (in cm). The mean size of the start aperture at movement onset in the different start aperture conditions are indicated by the black filled circles. All error bars depict ± 1 SEM (between subjects).

Figure 2: Experiment 1: Mean percentage of local minima indicating a dip in the aperture profile in the different start conditions. All error bars depict ± 1 SEM (between subjects).

Figure 3: Experiment 1: Representative single subject data showing a typical aperture profile (one trial) in the different experimental conditions: a) PG–condition and object size of 40 mm , b) SG–condition and object size of 55 mm, c) LG–condition and object size of 55 mm, d) FG–condition and object size of 40 mm.

Figure 4: Experiment 1: Mean time-normalized aperture profiles for the different start conditions.

Figure 5: Experiment 1: Averaged XY spatial paths over all participants for index, thumb and wrist in the different start conditions (the movement was executed from the left to the right side). The horizontal and the vertical lines show the standard deviation in x and y direction, respectively.

Figure 6: Experiment 1: The effect of start aperture size and object size on: a-d) the transport component of the movement (TPV, APV, TPD and APD); e) the average distance traveled by the thumb from movement onset to MGA, and from MGA to the touch of the object; f) the averaged normalized time until the occurrence of the MGA. All error bars depict ± 1 SEM (between subjects).

Figure 7: A: Schematic drawing of the setup of Experiment 2 (top view). The inset on the right shows the stimulus configuration used in Experiment 3. The stimuli were presented at the mid position. B: The four different start orientations of the aperture used in Experiments 2 and 3.

Figure 8: Experiment 2: Mean time-normalized grip rotation profiles for the different start orientations and object positions.

Figure 9: Experiment 2: The effect of start aperture size and object position on: a-d) the transport component of the movement (TPV, APV, TPD and APD); e): the average distance traveled by the thumb from movement onset to MGA, and from MGA to the touch of the object; f): the averaged normalized time

until the occurrence of the MGA. All error bars depict ± 1 SEM (between subjects).

Figure 10: Experiment 3: Mean time-normalized grip rotation profiles for the different start orientations and object orientations.

Figure 11: Experiment 3: The effect of start aperture size and object orientation on: a-d) the transport component of the movement (TPV, APV, TPD and APD); e) the average distance traveled by the thumb from movement onset to MGA, and from MGA to the touch of the object; f) the averaged normalized time until the occurrence of the MGA. All error bars depict ± 1 SEM (between subjects).

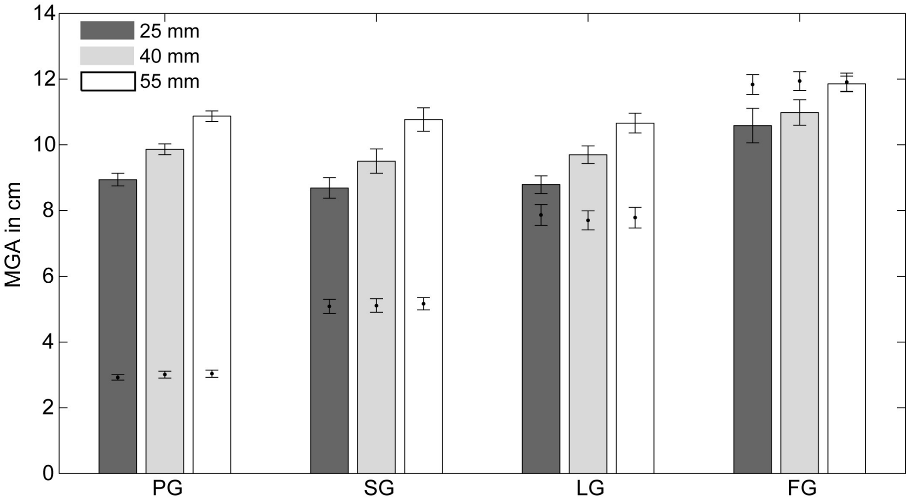
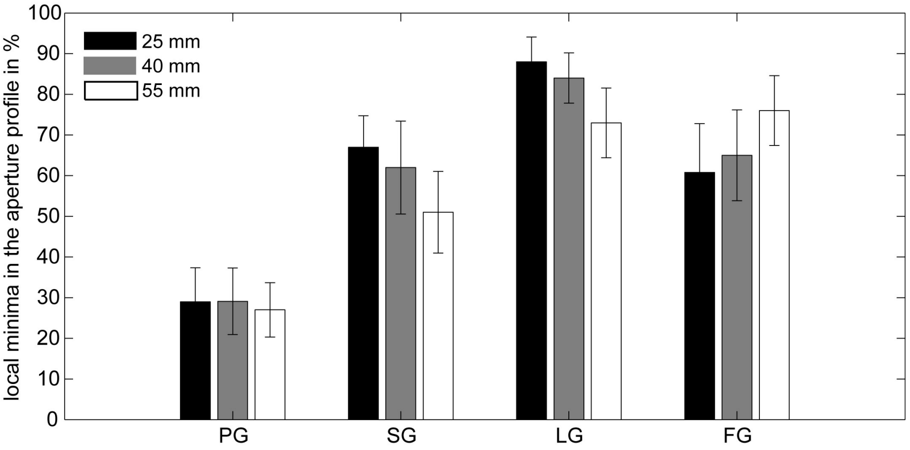


Figure 1


local minima in the aperture profile in %
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70
80
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25 mm
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55 mm
PG
SG
LG
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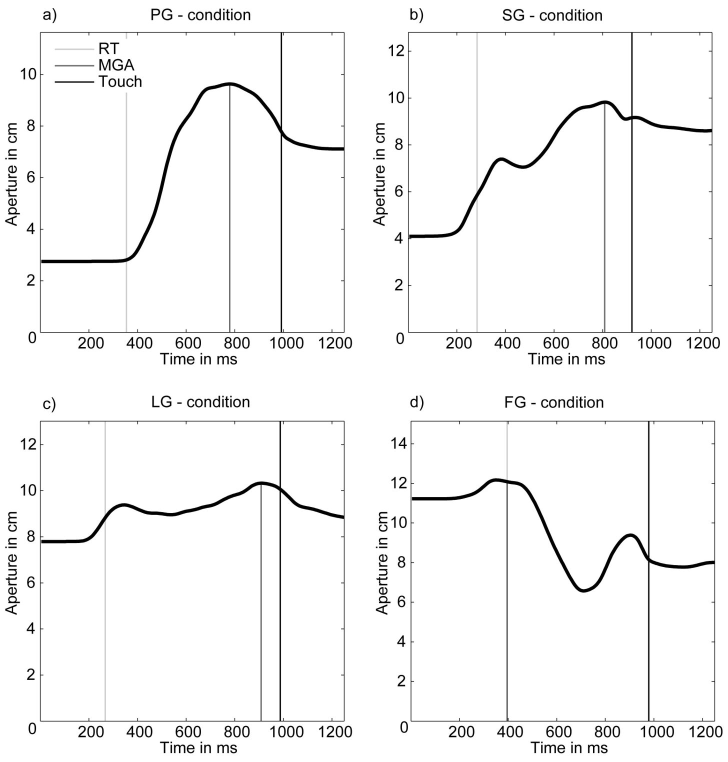
Figure 2


a)
PG - condition
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b)
SG - condition
Aperture in cm
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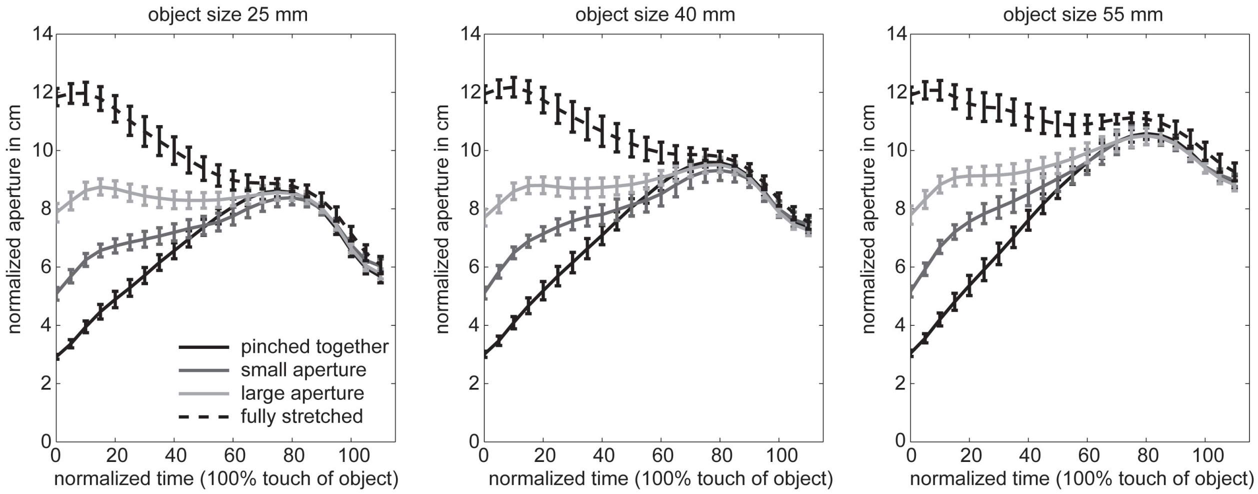
Time in ms
c)
LG - condition
Aperture in cm
0
2
4
6
8
10
12
200
400
600
800
1000
1200
Time in ms
d)
FG - condition
Aperture in cm
0
2
4
6
8
10
12
14
200
400
600
800
1000
1200
Time in ms

Figure 3

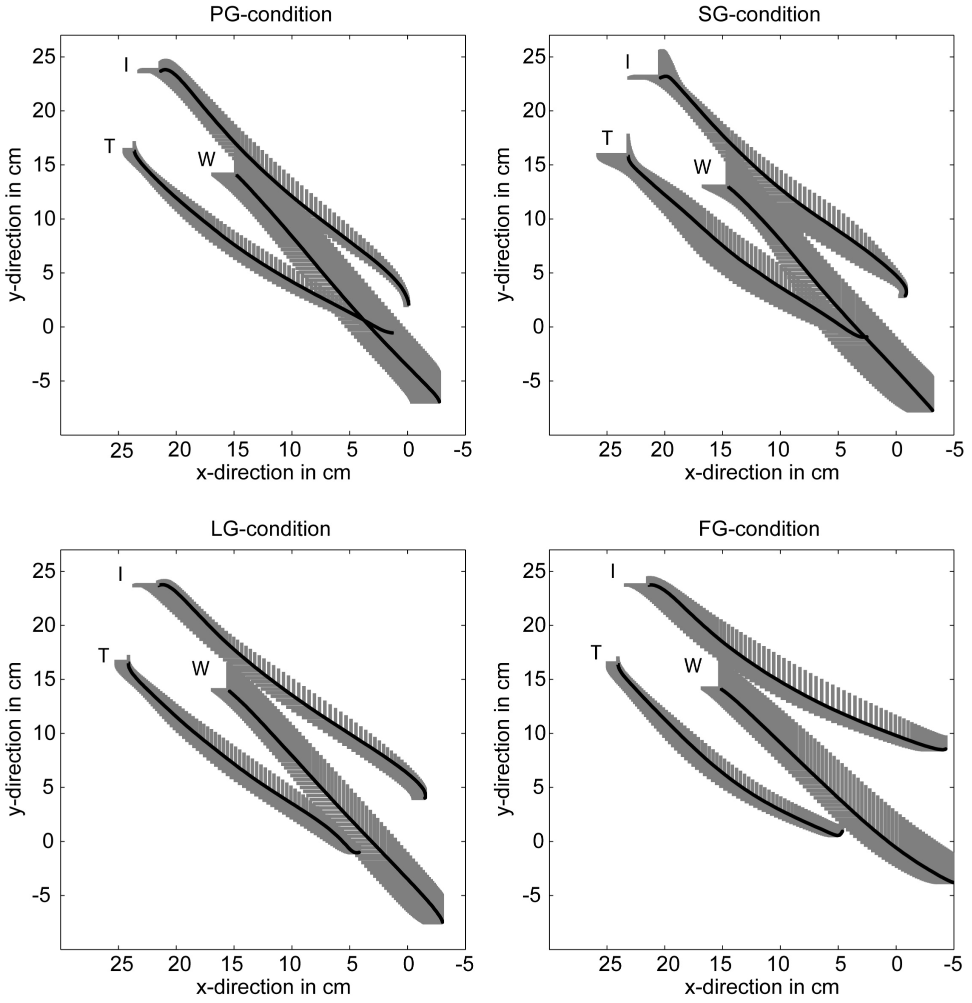


object size 25 mm

object size 40 mm

object size 55 mm

Figure 4


PG-condition

SG-condition

LG-condition

FG-condition

Figure 5

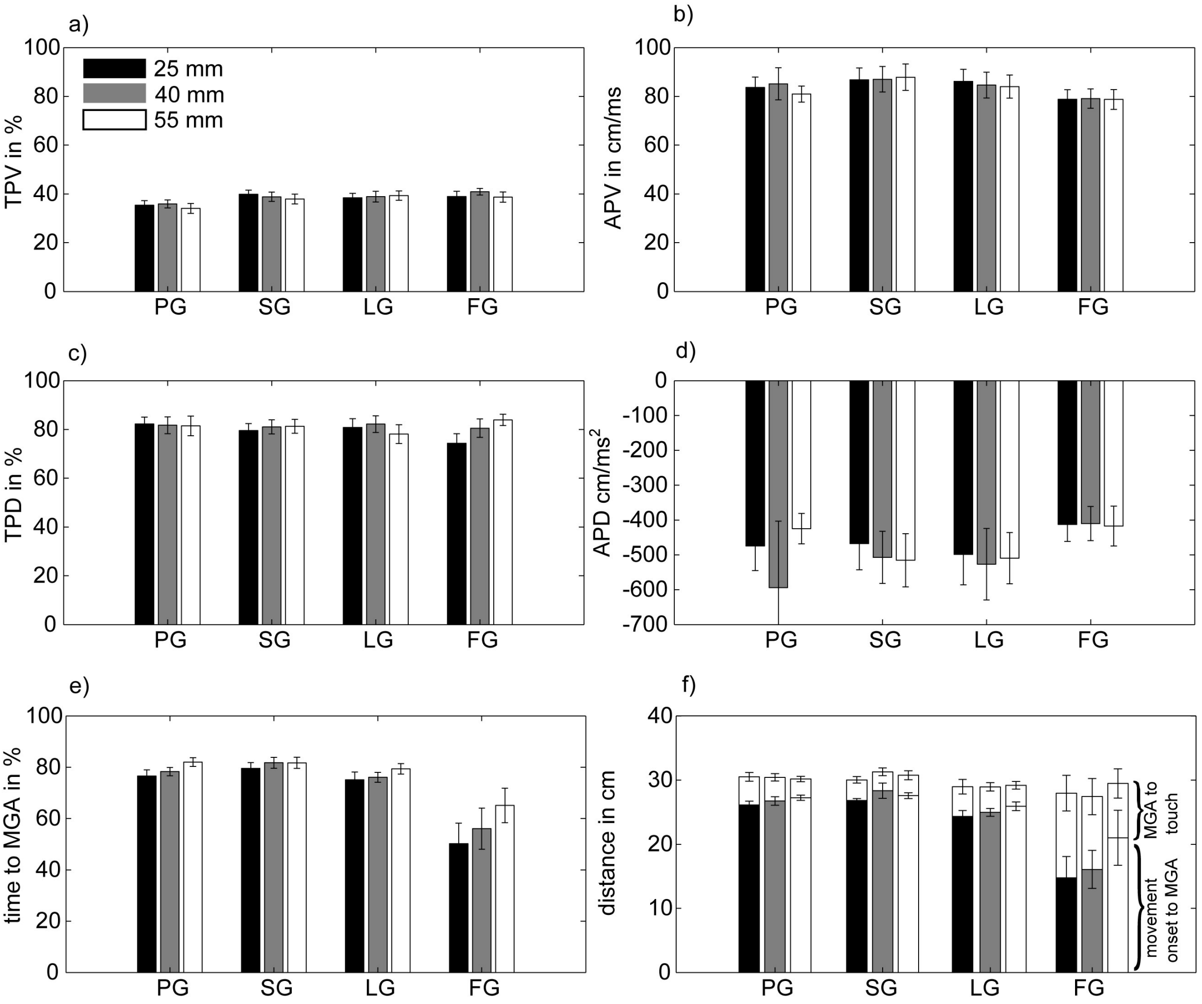

a)
TPV in %
25 mm
40 mm
55 mm
0
20
40
60
80
100
PG
SG
LG
FG
b)
APV in cm/ms
0
20
40
60
80
100
PG
SG
LG
FG
c)
TPD in %
0
20
40
60
80
100
PG
SG
LG
FG
d)
APD cm/ms^2
0
-100
-200
-300
-400
-500
-600
-700
PG
SG
LG
FG
e)
time to MGA in %
0
20
40
60
80
100
PG
SG
LG
FG
f)
distance in cm
0
10
20
30
40
PG
SG
LG
FG
MGA to touch
movement onset to MGA

Figure 6

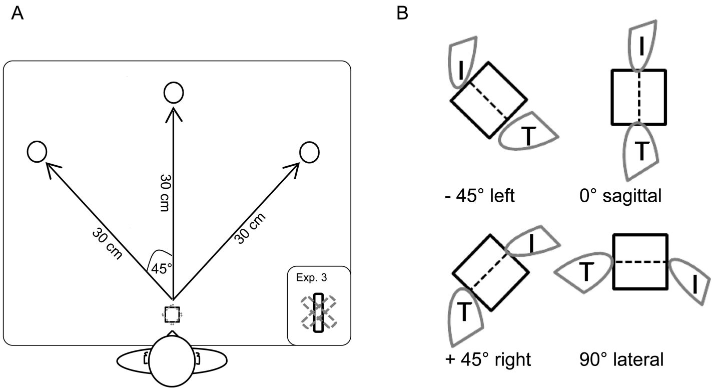

A
30 cm
30 cm
30 cm
45°
Exp. 3
B
I
T
- 45° left
0° sagittal
+ 45° right
90° lateral

Figure 7

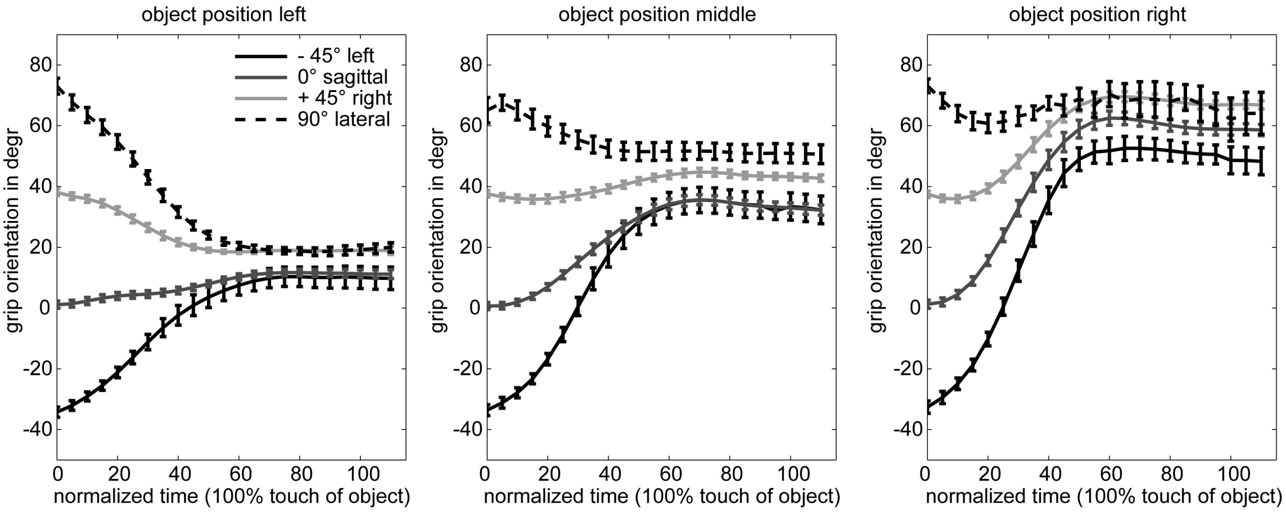

object position left
object position middle
object position right
- 45° left
0° sagittal
+ 45° right
90° lateral
grip orientation in degr
80
60
40
20
0
-20
-40
0
20
40
60
80
100
normalized time (100% touch of object)

Figure 8

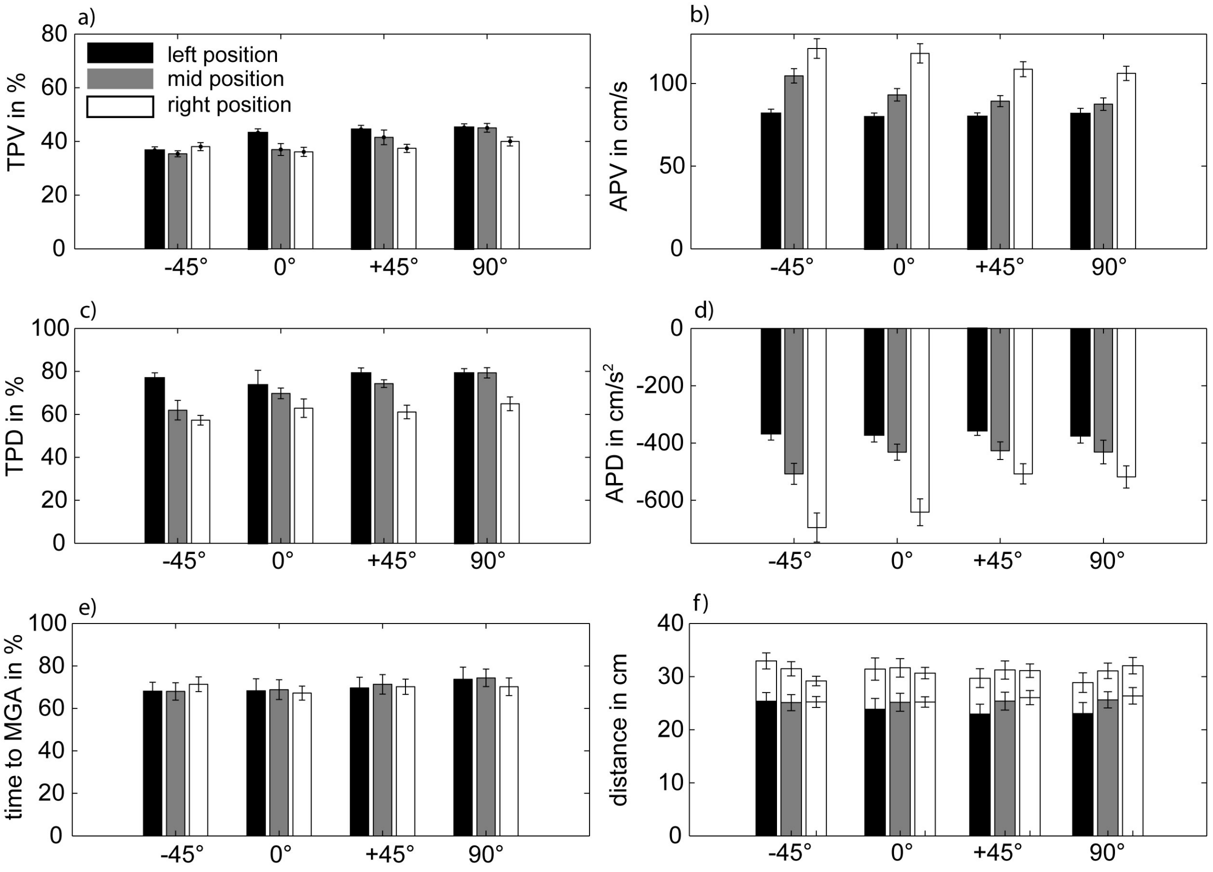

a)
TPV in %
80
60
40
20
0
left position
mid position
right position
-45°
0°
+45°
90°
b)
APV in cm/s
100
50
0
-45°
0°
+45°
90°
c)
TPD in %
100
80
60
40
20
0
-45°
0°
+45°
90°
d)
APD in cm/s²
0
-200
-400
-600
-45°
0°
+45°
90°
e)
time to MGA in %
100
80
60
40
20
0
-45°
0°
+45°
90°
f)
distance in cm
40
30
20
10
0
-45°
0°
+45°
90°

Figure 9

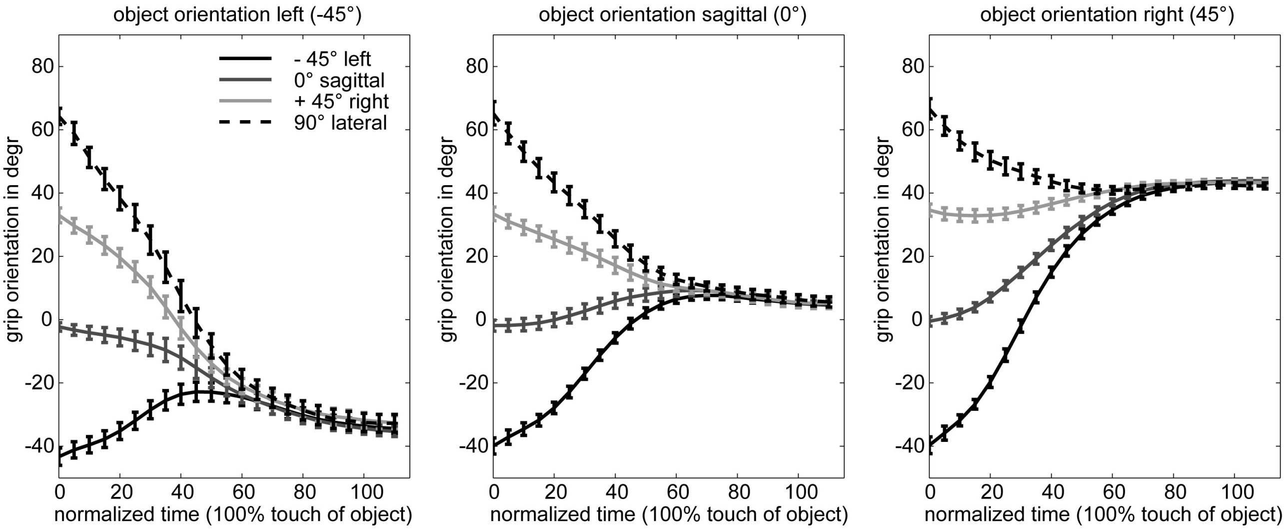

object orientation left (-45°)
object orientation sagittal (0°)
object orientation right (45°)
- 45° left
0° sagittal
+ 45° right
90° lateral
grip orientation in degr
normalized time (100% touch of object)
80
60
40
20
0
-20
-40
0
20
40
60
80
100

Figure 10

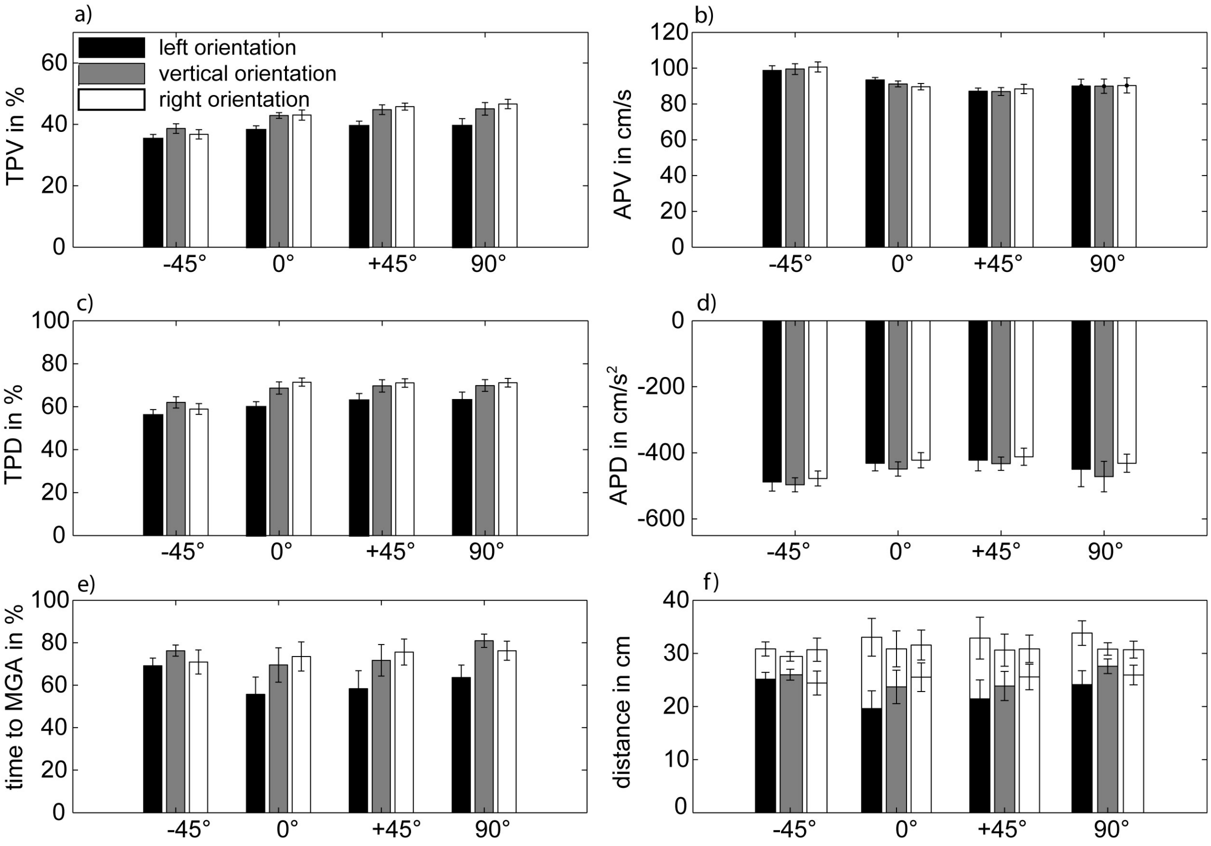
a)
left orientation
vertical orientation
right orientation
TPV in %
0
20
40
60
-45°
0°
+45°
90°
b)
APV in cm/s
0
20
40
60
80
100
120
-45°
0°
+45°
90°
c)
TPD in %
0
20
40
60
80
100
-45°
0°
+45°
90°
d)
APD in cm/s2
0
-200
-400
-600
-45°
0°
+45°
90°
e)
time to MGA in %
0
20
40
60
80
100
-45°
0°
+45°
90°
f)
distance in cm
0
10
20
30
40
-45°
0°
+45°
90°

Figure 11

Table 1

Experiment 1			
	main effect of start aperture size	main effect of object size	interaction
Transport			
APV	$F(3,27) = 3.2, p = .06$	$F(2,18) = 0.6, p = .51$	$F(6,54) = 0.9, p = .43$
TPV relative	$F(3,27) = 2.0, p = .15$	$F(2,18) = 1.0, p = .37$	$F(6,54) = 0.9, p = .49$
APD	$F(3,27) = 1.3, p = .29$	$F(2,18) = 0.7, p = .45$	$F(6,54) = 0.8, p = .42$
TPD relative	$F(3,27) = 0.4, p = .75$	$F(2,18) = 2.2, p = .14$	$F(6,54) = 2.6, p = .07$
Experiment 2			
	main effect of start aperture orientation	main effect of object position	interaction
Transport			
APV	$F(3,27) = 5.8, p = .02*$	$F(2,18) = 72.0, p < .001**$	$F(6,54) = 8.4, p = .001**$
TPV relative	$F(3,27) = 11.4, p = .001**$	$F(2,18) = 9.6, p = .002**$	$F(6,54) = 6.7, p = .001**$
APD	$F(3,27) = 6.1, p = .01**$	$F(2,18) = 70.2, p < .001**$	$F(6,54) = 4.9, p = .01**$
TPD relative	$F(3,27) = 4.2, p = .03*$	$F(2,18) = 36.5, p < .001**$	$F(6,54) = 2.8, p = .06$
Experiment 3			
	main effect of start aperture orientation	main effect of object orientation	interaction
Transport			
APV	$F(3,21) = 6.4, p = .01**$	$F(2,14) = 0.2, p = .73$	$F(6,42) = 1.3, p = .31$
TPV relative	$F(3,21) = 18.6, p = .001**$	$F(2,14) = 73.2, p < .001**$	$F(6,42) = 2.7, p = .09$
APD	$F(3,21) = 2.3, p = .14$	$F(2,14) = 1.6, p = .25$	$F(6,42) = 0.1, p = .98$
TPD relative	$F(3,21) = 11.3, p = .004**$	$F(2,14) = 34.4, p < .001**$	$F(6,42) = 1.9, p = .16$

APV: amplitude of peak velocity (cm/s); TPV: relative time to peak velocity (% MT)

APD: amplitude of peak deceleration (cm/s^2); TPD: relative time to peak deceleration % MT).

Results of the repeated–measures ANOVAs applied to different dependent variables characterizing the transport component.