Discussion
7.1 Summary and discussion

For grasping an object one needs to determine suitable positions on its surface for placing one’s digits, and subsequently to move the digits to these positions. Humans can select from many possible combinations of grasping points the most appropriate one for the given task. They can also move their digits along infinitely many ways to the selected grasping points. The relation between these two aspects of the grasping movement was studied in chapter 2, where subjects reached to grasp either short or tall objects. Subjects moved one of their digits over the short object whereas they curved it around the tall object. The two different movement trajectories resulted in similar grasping points, suggesting that the grasping points are selected before choosing the trajectory towards them. This, however, does not necessarily mean that the grasping points are selected on the basis of a control mechanism, like the equilibrium-point hypothesis, which only generates a movement trajectory only considering the endpoints, because otherwise the movement trajectories would not have been different for the different object heights. The grasping points were chosen independently of the movement trajectory towards them in chapter 2. This does not mean that any movement trajectory leads always to the same grasping points, since subsequent actions (Rosenbaum et al., 2012) or other constraints, like obstacles that influence the geometry of space (Rosenbaum et al., 2001), can influence the selection of grasping points.

Chapter 3 showed that when obstacles restrict the usual hand or arm grasping postures, subjects exploit the redundancy of their motor system to select grasping points other than the usual. Instead of moving their hand and arm along completely different trajectories to be sure to avoid the obstacle, subjects selected movements that led the hand or arm close to the obstacle, but also close to the usual grasping points. Such selection may have arisen because moving the arm to the right of the obstacle (instead to the left; see 118
figures 3.6 and 3.7) would require larger elbow and shoulder movements, and elbow movements have been associated with increased travel costs (Rosenbaum et al., 1995) or work (Soechting et al., 1995). Therefore, it may be more advantageous to select only slightly different grasping points and take more care not to hit the obstacle than to select a movement that is cost-inefficient. Grasping points are thus selected considering the constraints that the whole system needs to overcome and not only those imposed on the digits.

Constraints imposed on the arm’s posture were considered when selecting grasping points, but chapter 4 showed that the selection of grasping points is not sensitive to constraints imposed on whole-body posture. In that study, subjects were asked to stand either on a stable surface or on a piece of foam placed on this stable surface. In the latter case higher constraints were imposed on body posture. When standing on foam, subjects exhibited larger postural sway, probably because the proprioceptive signals from the foot were degraded, which led to more corrective movements being necessary so that a safe upright posture would be kept. Such constraints, however, did not affect the usual execution of the grasping movement or the usual selection of grasping points. This suggests that motor coordination may be hierarchically organized so that the performance of the most critical aspect of the movement is varied as little as possible from some standard performance, while other aspects are modified to facilitate the execution of the task.

The findings of the first three chapters underlie the importance of considering the constraints that are imposed on all body parts involved in the task. The selection of grasping points largely depends on the configuration of the hand and arm at the moment of the grasp under the studied circumstances. But do the selected grasping points lead to the selection of the final hand and arm posture, or is it the final posture that is first chosen and then some combinations of grasping points emerge? A clear answer cannot
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directly be given by the obtained results, mainly because the studies in this thesis were not designed to examine this issue. However, the grasping points are not just the outcome, but, instead, are the goal of a grasping movement, because their selection is crucial for the successful execution of the following task. Hand postures have been found to be neurally represented earlier than arm postures are (Klatzky et al., 1995). The movement toward the grasping points also become much less variable when the digits approach these points (Desmurget et al., 1995), presumably to ensure that the digits will be accurately placed on the grasping points. When moving the hand repeatedly to a target, people remember better the final position than the movement that led to this position (Marteniuk and Roy, 1972). These findings could altogether be interpreted as the grasping points being selected before the final configuration is.

To select grasping points, one needs to first identify the target object, and to consider obstacles that need to be avoided when guiding the digits to these points. To do so, visual information is essential. Yet, people appear not to select grasping points that are visible more often than grasping points that are invisible. In chapter 5 our subjects grasped a partly occluded object, which had a shape and orientation that was different in every trial. Our subjects did not specifically aim at grasping points that were visible. A reason to avoid visible grasping points in our case could be that subjects had to grasp the objects far from their preferred hand and arm configurations. Adopting a grasping posture away from extreme muscle and joint positions might have been a strategy when planning grasping points in that study, because this has been shown to be more advantageous for the control of the movement (Rossetti et al., 1994; Sood et al., 2007). However, our subjects could also have moved their head to be able to see the selected grasping points, but they did not do this either. Instead, they moved towards the usual grasping points more carefully, and relied on visually completing the partly occluded object (Sekuler, 1994).
Combining multiple sensory inputs and using this combination to plan and execute a movement is essential, because people interact with a continuously changing environment. For instance, when intending to grasp an object while walking, one needs to relate one’s body position and configuration with the object’s position. One needs also to consider that visual information is meanwhile changing continuously, and perhaps also consider other factors such as potential obstacles to the body or to the expected arm movement. Although this is a complex situation, one should be able to determine such relationships in a controlled environment, where no sudden changes occur. But people are also able to do so in situations where unexpected changes occur, adjusting for example their arm movements to sudden changes of the target object’s characteristics (Desmurget et al., 1996; Paulignan et al., 1997). Apparently, people are able to perform such adjustments despite the long processing times that the brain requires to analyze the changes that occur. In chapter 6, our subjects were able to initially adjust their grasping movement in response to a sudden change of the object’s orientation. In some trials about 40 ms after this initial response, subjects abandoned the response or even counteracted it, and planned completely different grasping points. These responses occurred with a latency of about 160 ms, with the digits ending at the most suitable grasping points at that time. Such latencies are much faster than the time it takes to initiate a movement as a response to the same visual stimulus (Smeets and Brenner, 1994). This is evidence that people are able to continuously consider complex relationships between various aspects of their movement and the environment during the execution of a grasping movement.

Corrective responses to unexpected perturbations while reaching have been suggested to be planned in the parietal lobe of the cortex (Desmurget et al., 1999; Tunik et al., 2005). This part of the brain receives information from the visual cortex through the so-called dorsal stream (Milner
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and Goodale, 1992). This stream is associated with controlling the eyes and the arm when movements are planned, and with representing spatial locations of objects. Patients with lesions in that part of the brain, like the famous patient A.T. (Jeannerod et al., 1994), cannot exhibit smooth and skillful grasping movements, but they are able to recognize the object that is to be grasped. This paradoxical behavior may originate because the object identification occurs in another region, the temporal lobe, where information from the visual cortex arrives through the ventral stream (Milner and Goodale, 1992). Another famous patient, D.F., with lesions in the occipitotemporal lobe is unable to recognize an object, but she can grasp it naturally. However, there is some debate about whether the visuomotor transformations can be so simply described by two independent visual streams. For instance, it has been suggested that the smooth grasping movements that D.F. can exhibit are mainly due to the haptic feedback she receives when her digits are placed on the object (Schenk, 2012).

The separation of the visual system in these two distinctive pathways has some similarities with the classical approach of grasping (Jeannerod, 1981). Indeed, the transport component that leads the hand towards the object has been suggested to depend on visual information about the location and the orientation of the object, information that is under the control of the dorsal stream. Meanwhile, the grip component that is responsible for the formation of the grip to match the object’s characteristics is suggested to depend on visual information about the object’s size and shape, information that flows through the ventral stream. This relation between the two visuomotor channels and the two grasping components makes the classical approach of grasping very attractive. Is this, however, reasonable and so simple?

7.2 Components or digits?

As also mentioned in the introduction, the main goal of a grasping movement is its end: the placement of the digits at suitable grasping points.
How the digits’ trajectories emerge and lead the digits to this end is a matter of debate. Jeannerod (1984) proposed that the hand moves towards the object and, independently of this movement, the digits move relative to each other so that the object is grasped. Smeets and Brenner (1999) came up with an alternative idea according to which grasping emerges by just moving the digits more or less independently towards predetermined positions on the object’s surface.

The independence between the components of the classical approach seems to have been violated in some experiments (Marteniuk et al., 1990; Paulignan et al., 1991). This has been interpreted by Jeannerod (1999) as the transport component having some influence on the grip component, but not the reverse. In chapter 3 of this thesis, movement time was increased when an obstacle constrained the placement of one of the digits on the object (figure 3.5c), placement that can be considered as being part of the grip component. The longer movement times found in chapter 3 are inconsistent with what one would expect if there was only an effect of the transport on the grip component. Such an increase of movement time could be a result of the obstacle imposing constraints on the individual digits’ movement trajectories. However, different movement trajectories do not necessarily lead to modifications in movement time, as shown in chapter 2 (figure 2.9b). If the placement of individual digits can be considered as being part of the grip component, constraints in this component that do lead to such modifications could then be interpreted as people controlling their digits (Smeets and Brenner, 1999; Biegstraaten et al., 2003).

According to the classical approach, moving the hand towards the object is part of the transport component, whereas the movements of the digits relative to each other are part of the grip component. However, to get a stable grip, the hand needs to be oriented in a way that the grip orientation will match the orientation of the object (Cuijpers et al., 2004). The orientation of an
object is a property that has been shown to affect the kinematics of both the transport and grip components (Desmurget et al., 1996; Gentilucci et al., 1996). Since the classical approach of grasping assumes no interactions between the components, object orientation is sometimes considered to be part of a third (independent) component (Stelmach et al., 1994).

The limitations of the classical approach may make the idea of grasping emerging by simply moving the digits to predetermined positions more attractive. However, it does not mean that considering grasping simply as pointing with two digits completely captures all the features of such a complex movement. In an attempt to more directly determine whether grasping is controlled separately by specific brain regions we tried to use a multivariate pattern analysis (MVPA; Haxby et al., 2001) in a functional MRI study comparing grasping with two-digits pointing\(^1\). fMRI imaging on three subjects revealed no differences in brain activity patterns between a precision grasping movement and a two-digits pointing movement, supporting the idea of grasping being planned and controlled as pointing is. However, just moving the hand to the object also led to similar activity patterns, so the evidence was not conclusive. Moreover, the previous chapters have shown that one needs to consider complex movements, such as grasping, as a movement in which the whole system is involved. Such an approach is difficult to be incorporated in simple models, so more complex ones are needed (Rosenbaum et al., 2001). Simple models that can predict a large portion of obtained results have one important advantage: their simplicity. This simplicity may, however, be also a limitation because grasping is a much more complex movement than moving the hand or the digits towards the

\[\text{The results of this study are not published and were obtained during a collaborative project between VU University Amsterdam and Royal Holloway University of London, in which Prof. Andy Smith, Eli Brenner, Marco Bartolucci and the author of this thesis were involved.}\]

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object’s surface, and that involves multi-segmental rotations, considerations of obstacles and satisfaction of different task demands. Nevertheless, although a more elaborate model may describe human motor and grasping behavior more completely, it does not necessarily describe grasping movements more accurately than a simple one (Smeets and Brenner, 2002).

It is important to realize that none of the two main frameworks make any prediction about the selection of grasping points. The classical approach assumes that an opposition axis is built into the grip component (Mon-Williams and Bingham, 2011), but it does not specify on what basis this opposition axis is built. Similarly, the two-digits framework assumes that appropriate grasping points have already been selected before the onset of the movement. Since neither of the frameworks considers the selection of grasping points, it is hard to validate either of the two from the results obtained in this thesis.

7.3 Concluding remarks

The human motor system is very complex and extremely flexible. People use many different sensory inputs to produce a plethora of movements and to complete a motor task in many different ways. Yet, grasping movements are quite stereotyped and people show strong consistencies in the selection of grasping points. Multi-perspective approaches are being employed to study what the control mechanisms of complex movements are. Computational models can help determine what causes specific aspects of human motor behavior. Studying the kinematic and neurophysiological behavior of patients provides more insights into the basis of the movement organization and the observed behavior. Important outcomes can also be inferred by comparing populations whose neural systems show differences, such as children and the elderly.
The outcomes of this thesis are hard to be directly used in the everyday world. Studying basic aspects of motor behavior does not usually result in applied findings, but rather in gathering more information about a system or building more on existing knowledge. Fundamental research on grasping explores the basis on which the observed behavior emerges. More specifically, exploring how and why the grasping points are selected might be useful in new technologies, prosthetics, or ergonomics. But the experiments presented here were designed to acquire more knowledge and understanding about the determination of complex aspects of a movement in the presence of several kinds of constraints. This thesis focused on what basis the selection of grasping points is made on, selection that needs a multimodal integration of different information. It is shown that the endpoints of the movement are selected independently of the movement towards them as well as of their visibility. It is also shown that people can exploit the motor system’s flexibility to plan different grasping points when the constraints are known in advance, but also that they can recruit this flexibility to overcome unexpected changes during the ongoing movement and quickly plan new positions at which their digits will end.
Discussion