Mechanisms of visual salience and memory on reaching and grasping behavior

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Contents

Summary

To interact successfully with our surrounding, human beings have the ability to manipulate their environment with their hands and legs. The present thesis aims at investigating the perceptual influences on action by providing evidence for the following questions: (i) how does visual salience influence both movement planning as well as movement execution in visually guided pointing movements, (ii) to what way are memory traces of motor programs stored during consecutive grasping movements, and (iii) how are grasping movements influenced by the way objects are encoded?

Chapter 2 & 3 investigated the influence of the salience map on visually guided pointing movements. Visual salience maps have been shown to mediate target selection in a number of visual search tasks. To examine known modulations in different visual search paradigms, a number of experiments were conducted. The results indicated that salience map signals are also used to program visually guided pointing movements. Whether ongoing visually-guided pointing movements are also influenced by the salience map was examined in Chapter 3. The duration to complete a movement successfully increased with decreasing saliency of the target. The findings of Chapter 3 are then integrated into current theories of motor control together with the theoretical concept of the salience map, thereby extending the perception-action framework from movement planning to movement execution.

In Chapter 4, the differential effects of memory on grasping behavior were investigated with evidence that objects are stored in memory in a location-unspecific manner. This is first evidence that movement parameters of previously grasped objects are stored in a feature-based manner, not bound to a specific location.

To understand how current visual input influences our actions, grasping movements of human beings were recorded using the visuomotor priming paradigm. The results of Chapter 5 suggest that visuomotor priming does not occur automatically by merely viewing

objects in the visual scene, but the relevant feature of the cue object has to be task-relevant as well. Chapter 5 provided new evidence in how human beings form motor representations when acting upon objects.

In summary, the thesis provided new evidence of the strong interaction between the perception and action systems, by showing that (i) movement planning and execution are guided by the salience map, (ii) object features are stored in a location-unspecific manner during grasping and (iii) visuomotor priming is not automatic during visually-guided grasping.

Contributions to this doctoral thesis

Chapter 1

The author of this doctoral thesis wrote Chapter 1. Michael Zehetleitner and Hermann J. Müller commented on the chapter.

Chapter 2

The author of this doctoral thesis contributed to Chapter 2 by designing the experiments, conducting and analyzing the data and writing the chapter. Michael Zehetleitner assisted in designing and analyzing the data and Hermann Müller supervised the project. The results were discussed by the author of this thesis, Michael Zehetleitner and Hermann J. Müller. A version of this chapter has been published as Zehetleitner, M., Hegenloh, M., & Müller, H. J. (2011). Visually guided pointing movements are driven by the salience map. *Journal of Vision, 11*, 24.

Chapter 3

The author of this doctoral thesis contributed to Chapter 3 by designing the experiments, conducting and analyzing the data and writing the chapter. Michael Zehetleitner assisted in designing and in the conceptual part of the chapter and Hermann Müller supervised the project. The results were discussed and the chapter was commented by the author of this thesis, Michael Zehetleitner and Hermann J. Müller.

Chapter 4

The author of this doctoral thesis contributed to Chapter 4 by designing the experiments, conducting and analyzing the data and writing the chapter. Constanze Hesse helped with technical support and the programming of the experiment. Michael Zehetleitner assisted in the conceptual part of the chapter and Hermann Müller supervised the project. The results were discussed and the chapter was commented by the author of this thesis, Michael Zehetleitner, Constanze Hesse and Hermann J. Müller.

Chapter 5

The author of this doctoral thesis contributed to Chapter 5 by designing the experiments, analyzing the data and writing the chapter. Lisa Pfannmüller conducted and analyzed the experiments in Chapter 5. Michael Zehetleitner assisted in the conceptual part of the chapter and Hermann Müller supervised the project. The results were discussed and the chapter was commented by the author of this thesis, Michael Zehetleitner, Lisa Pfannmüller and Hermann J. Müller.

Chapter 6

The author of this doctoral thesis wrote Chapter 6. Michael Zehetleitner and Hermann J. Müller commented on the chapter.

The above contributions to the doctoral thesis of Michael Hegenloh are all correct as stated above.

Hermann J. Müller

Michael Zehetleitner

CHAPTER I

General Introduction

General Introduction

To survive in our complex environment, human beings are equipped with a nervous system to process all kinds of information from the environment and a motor system to interact with and manipulate our environment. The human visual and auditory system act as a filter to separate important from non-important information (e.g., Carrasco, 2011) and thus makes it possible to navigate and interact with other human beings and the surrounding human beings are exposed to. Visual information is processed in a manner that is influenced both by the background context the human organism is situated and its current intentions and goals. Even though in the past two decades the idea has become prominent that action and perception have to be considered as one highly interlinked system rather than two independent systems (e.g., Hommel, Müsseler, Aschersleben, & Prinz, 2001; e.g., Prinz, 1984; Rizzolatti & Craighero, 2004), most research has focussed exclusively either on perception or action. This thesis specifically examined the manner in which visual information is capable of influencing our motor behavior.

In the following, I introduce the theoretical concept of a salience map (e.g., Itti & Koch, 2001) a construct to simulate and predict what aspects of the visual scene are most likely to be selected by attention, in conjunction with behavioral and neurophysiological findings. The second part will cover human movement planning in general and decision making in the context of human movement planning.

Salience Maps

What is salience and what are salience maps? Salience is most commonly defined as stimulus-driven conspicuity or distinctiveness of an object (Itti & Koch, 2001). The conspicuity of an object in the visual scene can stem from its size, orientation, luminance, movement and other features (for a review, see Wolfe & Horowitz, 2004). Importantly, conspicuity is not solely dependent on the object in the visual scene itself, but especially on its relation to the context, like other objects in the display, the background of the visual scene and the intention or task specifications (Gottlieb, 2007). The salience map is the output of summing up all conspicuities of the object in the visual scene, by giving each object a salience value independent of its feature (Koch & Ullman, 1985). This summation of salience values includes several steps: (i) the visual scene is analyzed regarding its specific feature (e.g., red, blue, vertical, horizontal) into various feature maps, (ii) the different feature maps are then summed up into dimension specific maps (e.g., color, orientation, motion) and finally (iii) integrated into a master saliency map which indicates the most salient location in the visual scene (Itti & Koch, 2001). The most salient location is then further analyzed by attending to the specific location respectively making an action towards that location (e.g., an eye movement; Thompson & Bichot, 2005). Over the past decade, behavioral and neurophysiological evidence have established similar conclusions (Fecteau & Munoz, 2006).

Behavioral and neurophysiological evidence. The concept of the salience map is a theoretical construct which accounts for many findings using a number of paradigms and methods. Most studies exploring the neurophysiological undermining of visual section have been done monkeys which allow for high spatial and temporal resolution Interestingly, the functional neuroanatomical foundations of the salience map has hitherto been identified among a wide variety of areas such as area V1 (e.g., Koene & Zhaoping, 2007; Li, 2000; Li, 2002), area V4 in the ventral stream (Mazer & Gallant, 2003), the superior colliculus (SC; Shen & Pare, 2007), the frontal eye fields (FEF: Thompson & Bichot, 2005), as well as in the lateral intraparietal area (LIP; Gottlieb, 2007). These areas are all highly interconnected and seem to fulfill different tasks for the saliency map (e.g., Pare & Wurtz, 1997). There is evidence that area V4 provides the necessary visual input to the FEF, the SC and the LIP (Lock, Baizer, & Bender, 2003; Mazer & Gallant, 2003).

Most prominent theories and models describing and including the concept of saliency maps are Guided Search (Wolfe, 2007) and the computational model of visual attention by Itti and Koch (Itti & Koch, 2001). The visual search paradigm has been widely used for investigating salience maps (see also Chapter 2 of this thesis for a more detailed description), complementing and extending the theoretical construct of the salience map and stimulating further neurophysiological studies (Mazer & Gallant, 2003). In a visual search task, observers have to find a target item among a number of distracters in the visual display, either as fast as possible by measuring reaction times (RTs) or as accurate as possible by measuring accuracy. Visual search is efficient (when adding distracters to the display does not influence RT), if the target item generates the highest salience value on the salience map, thus leading attention first to the target location as compared to when all item in the display generate the same salience value (inefficient search; M. Bravo & Blake, 1990). Current visual search models (Itti & Koch, 2001) did not include any kind of memory in their search models, meaning that each search, from one trial to the other, starts by resetting the system. Contrary to the predictions of visual search models, it has been found that varying the target dimension (e.g., color and orientation) from trial to trial, search RTs increased when the target defining dimension changed as compared to when it was repeated from trial to trial (Found & Müller, 1996; Müller, Heller, & Ziegler, 1995; Müller, Reimann, & Krummenacher, 2003). These intertrial RT effects have been termed *dimensional weighting* and have been integrated into the theoretical salience map framework. It is assumed that (i) dimensional weighting effects arise at an early preattentive processing stage (Zehetleitner & Müller, 2010) and (ii) dimension-specific feature contrast signals are weighted before the integration into the master saliency map. If only one dimension occurs in a number of successive trials, then this dimension is weighted (up-regulated) and the target will be found faster (in comparison with changing dimensions from trial to trial). Recently, top-down control was included into the formulation of saliency map models (Melloni, van Leeuwen, Alink, & Muller, 2012; Saalmann, Pigarev, & Vidyasagar, 2007; Töllner, Zehetleitner, Gramann, & Müller, 2011; Wolfe, 1994), which highlight the influence of the current task on guiding attention and eye movements (Baluch & Itti, 2011).

Influence of saliency on eye movements. Saccadic eye movement involve a number of brain areas (LIP, FEF and SC) that have been found in the generation of saliency signals as well (Fecteau & Munoz, 2006). Thus the question arises whether eye movements are directed to the most salient locations in the visual scene? The computational saliency model by Itti and Koch (2001) predicts the following: (i) visual attention and saccadic eye movements are directed to the most salient location in the visual scene; (ii) after shifting attention or making an eye movement to that location, this location is subsequently inhibited in order to facilitate a shift of attention to the second most salient location, and (iii) this mechanism allows for dynamically controlling eye movements and attention according to local saliency differences in the visual scene. Neurophysiological evidence has demonstrated that the monkey brain uses saliency signals from LIP to guide saccades in a visual search task (Goldberg, Bisley, Powell, & Gottlieb, 2006). On the neuronal level, the LIP has been correlated with shifts of attention to locations in space in addition to being able to transiently move the locus of attention away from the target location when there is a distractor in the visual field (Bisley & Goldberg, 2003). Thus, the LIP signals relevant locations in space (like the concept of the saliency map), which can be used to guide attention and eye movements under conditions when the locations are relevant to the task demands (Goldberg, et al., 2006). There is psychophysical evidence as well that saccadic eye movements are driven by the saliency map (Parkhurst, Law, & Niebur, 2002). In the study by Parkhurst, Law and Niebur, participants were told to freely explore the natural image with no specific task. The correlation of visited saccadic locations and visual salience of the image was best right after the onset of the trial and got weaker as the trial continued. This correlation shows the influence of intentional or top-down control when viewing the image longer than just a second. In many recent studies and models of visual search, top-down control is included as an influential factor guiding eye movements as well as attention (Baluch & Itti, 2011).

Movement planning

Planning and executing a goal-directed hand movement is a complex process involving many different mechanisms, ranging from localizing the target object in visual space, to knowing the position of the effectors (e.g., hands and legs) and finally planning the trajectory of the desired movement. The literature is, to my knowledge, divided into two different levels for explaining movement planning. One line of literature approaches the problem from the motor control side (e.g., Desmurget, Pelisson, Rossetti, & Prablanc, 1998), whereas others use psychophysiology to explore the psychological aspects of movement planning (e.g., Milner & Goodale, 2006). Both ways of explaining movement planning are illustrated below.

Visuomotor transformations from the motor control view. When grasping an object, the position of the object in space is encoded first in relation to the eye position and is then it is transformed into a coordinate system which provides a frame of reference whose function is to plan and execute the movement of the effector.

The first step is to encode the target in egocentric coordinates, which is the information relative to where the organism is in in space. If we move, turn our head or turn around, egocentric coordinates will always be transformed accordingly. To localize a target object in space, retinal information, as well as extra-retinal information are combined in a co-active manner for accurate target localization (Bock, 1986). There is evidence that both retinal as well as non-retinal information produce better target localization accuracy when combined, instead of using each information source alone (Bock, 1986). Information about eye and head position is provided from two different sources: eyes mainly use efferent signals (motor signals from the central nervous system to the peripheral nervous system are called efferent signals), while the head position uses mainly sensory information (from the vestibular system) to code the rotation. Using egocentric target coordinates, the position of the eyes and head, it is possible to transform these egocentric coordinates into an allocentric coordinate system (Byrne, Becker, & Burgess, 2007). An allocentric reference frame is independent of the viewer and is coded in world coordinates.

The second step in generating successful visually-guided movements is to determine the position of the arm. Evidence from this necessity is coming two lines of research: (i) patients without proprioception were not able to accurately perform movements (Ghez, Gordon, & Ghilardi, 1995) and (ii) electrophysiological studies showed that initial arm position is coded in the parietal and the motor cortex and that the coding of the target location is influenced by the current position of the arm (Georgopoulos, Caminiti, & Kalaska, 1984; Kettner, Schwartz, & Georgopoulos, 1988). Thus, programming the initial position of the arm seems to be a necessary step for movement planning.

The last step in the movement plan is the trajectory programming. Here I will briefly summarize the three major theories on trajectory formation: (i) the equilibrium-point hypothesis, (ii) the population coding vector hypothesis and (iii) the optimal control hypothesis.

The equilibrium-point hypothesis is best explained when visualizing a robot made out of rubber bands instead of motors for each joint. When releasing the robot's arm after bending it in one direction, it will always settle in the same configuration. This configuration is called the equilibrium point of the system and can be compared to the human muscle properties. If both the agonist and antagonist muscle of the arm are balanced, then the equilibrium point of the arm is reached. When reaching to an object, the equilibrium point of the arm is changed continuously, in order to smoothly grasp the object. The equilibrium-point hypothesis was first introduced by Feldman (1986) and has been further developed to account for multiple joint movements (Bizzi, Hogan, Mussaivaldi, & Giszter, 1992). This trajectory formation hypothesis has been modeled and movement trajectories were predicted from the simulated data (Flash, 1987).

The second line of research focuses on the population coding vector hypothesis (first introduced by Georgopoulos, Kalaska, Caminiti, & Massey, 1982), describing trajectory formation at a neuronal level. While monkeys performed a pointing task, neuronal activity was measured in the motor cortex. It was observed that individual neurons fired preferentially for one direction over another, and these response properties were called preferred directions. Interestingly, there was not a one-to-one mapping of neurons to a specific direction. Rather, populations of neurons coordinated their response properties such that, when taken together, their collective response coded a specific direction. This led Georgopoulos et al. to formulate a population vector that could predict the direction and the amplitude of the movement. This finding has been replicated and extended in a number of studies (e.g., Georgopoulos, Kettner, & Schwartz, 1988; Schwartz, 1994).

The third group are models uses optimization principles from the optimal control theory and is explained using the minimum torque change model (Uno, Kawato, & Suzuki, 1989) - a prominent model guided by optimization principles. The idea behind these kinds of models is that each reaching and grasping movement has an infinite number of possible reach trajectories and velocity profiles. How do we select one possible trajectory out of the many possibilities? The models using optimization principles take the trajectory with the smallest possible costs involved in the movement (Flash & Hogan, 1985; Körding & Wolpert, 2006; Todorov, 2004). According to Uno et al. (1989), the minimum torque change model is using a minimized cost function to predict the torque change during the movement. With this mathematical formulation of the model, velocity profiles as well as the curvature of the movement can be predicted from the direction and the amplitude of the movement.

Visuomotor transformations from the psychological view. The psychological literature has taken a strikingly different perspective to describe and explain visuomotor transformations. The primary differences between the motor control and psychological literatures are that, within psychology, movement planning is understood in terms of different cognitive architectures, whereas researchers working in motor control have focused on explaining trajectory formation and the motor apparatus itself. The following section is explaining the perception-action model introduced by Ungerleider and Mishkin (1982). The *two-visual systems hypothesis* is a model for the dissociation between vision for action and vision for perception (Milner & Goodale, 2008), which was build upon evidence from patients with either lesions in the dorsal or ventral stream. A lesion in the ventral stream was accompanied with accurately reaching and grasping for objects, but with the incapability of discriminating objects (T. W. James, Culham, Humphrey, Milner, & Goodale, 2003). However, patients with damage in the dorsal stream are not able to reach or grasp accurately (Karnath & Perenin, 2005). Following these two studies, it seems that vision for action and vision for perception is separated in healthy human beings. At some point in time and neuroanatomy, the two streams have to interact since the visual-for-perception grounds visual awareness, informing the vision-for-action pathway about what movements to program (Milner & Goodale, 2008). Vision-for-action is capable of programming movements by transforming afferent visual information into motor programs, while vision-for-perception pathway is used for the planning of movement. Basic properties of the perception-action model are shown in Table 1 (according to descriptions by Milner & Goodale, 2008).

Table 1. Overview on the basic features of the perception-action model (adapted from Schenk and McIntosh, 2010)

dorsal stream	**ventral stream**
vision for action	vision for perception
egocentric reference frame	allocentric reference frame
no memory	ability to store in memory
no awareness	conscious awareness

Different reference frames. An important distinction between the dorsal and ventral stream is the encoding of spatial information. As in the model described, the ventral stream codes spatial information in an allocentric reference frame and the dorsal stream codes spatial information in an egocentric way. Evidence for this comes from an fMRI study (Valyear, Culham, Sharif, Westwood, & Goodale, 2006) contrasting objects which varied in identity, orientation or both features. A double dissociation has been found with the ventral stream being affected only by the identity of the object, whereas the dorsal stream was influenced only by the orientation of the object. The distinction between dorsal stream coding in an egocentric way and ventral stream coding in a allocentric way is still not clear, since a number of studies support this distinction (see Logothetis & Sheinberg, 1996, for a review), whereas others make the reverse claim - namely, that the dorsal stream encodes space allocentrically (Snyder, Grieve, Brotchie, & Andersen, 1998).

Memory within the perception-action model. Within the perception-action model according to Milner and Goodale (2006), visuomotor programs represented in the dorsal stream - via afferent vision - decay very rapidly, while ventral stream representations can be stored in long-term memory (Westwood & Goodale, 2003). The debate about the involvement of both the ventral and the dorsal stream in programming movements is further developed in Chapter 4 of this thesis.

Milner and Goodale’s (2006, 2008) standard perception-action model, which defines two independent processing streams, has been forced to extend itself given the increasing evidence that the ventral and dorsal streams interact and cross-talk with each other (e.g., Farivar, 2009).

Decision making in movement planning

The question I now turn to concerns the selection of action, or decision making processing involved when choosing among the number of possible alternative actions. The difference between the first chapter on salience maps and this chapter is that the output, according to the literature, can only be interpreted to guide attention or eye movements to a specific location in space, either controlled by bottom up stimulus signals or top down intentions (Fecteau & Munoz, 2006), but not while planning possible reaching or grasping movements. An influential account is explained here, merging both the processes of movement selection and movement programming and trying to explain a number of findings from different areas of research (Cisek, 2007). According to the affordance competition hypothesis, action selection and action specification occur at the same time. Action specification is the process of transforming sensory object information into possible movement programs (for a detailed description on the transformation, see the Movement planning section) with involvement of the dorsal stream (Goodale & Milner, 1992), including a number of brain areas in the posterior parietal and frontal cortex (Andersen & Buneo, 2003; Pesaran, Nelson, & Andersen, 2008). Both the frontal and parietal cortex are able to represent possible movement goals and have the ability to bias the selection to one of the alternative action goals (Pesaran, et al., 2008). This competition is thought to be influenced by a number of factors, including the possible value of the action (Padoa-Schioppa & Assad, 2006), reward (Schultz, 2004) and task (Sakagami & Pan, 2007). According to Cisek (2007), the affordance competition hypothesis is in agreement with at least two computational models on simple decision making (Gold & Shadlen, 2007; Roger Ratcliff, Hasegawa, Hasegawa, Smith, & Segraves, 2007). These so called diffusion models separate incoming evidence according to decision criteria and other non-decision criteria such as stimulus processing. When diffusion models are applied within the context of movement planning, several possible alternative movement choices will race against each other until one has reached the threshold, at which point a decision is made. In summary, the affordance competition hypothesis is a model of human interactive behavior, which include many possible action choices at the same time that are all represented simultaneously and compete for selection (Cisek, 2007; Cisek & Kalaska, 2010).

Scope and summary of the thesis projects

The purpose of this thesis is to investigate what attributes guide human movement planning and execution. Following the introduction, salience maps have the ability to guide attention and eye movements (Baluch & Itti, 2011) and from electrophysiology it is known that decisions about attention shifts and eye movements are coded in the same brain areas as eye movements and attention shifts are generated (Gold & Shadlen, 2007; Schall & Bichot, 1998). The posterior parietal cortex (PPC), which is responsible for planning reach movements, and the LIP, which is responsible for planning eye movements, have both been shown to process information in a similar manner, such that both may operate within the same network (Andersen & Buneo, 2003). Following this line of argumentation, is it possible that the PPC processes information coming from the salience map? Based on the evidence of the target stimuli, movements which have already been executed can still undergo adjustment during the movement through feedback from visual information (Resulaj, Kiani, Wolpert, & Shadlen, 2009). Chapter 2 investigates the influence of visual salience on movement planning, while Chapter 3 explores if visual salience has the ability to influence already executed movements. With visual salience being the main factor to influence movement planning and execution in Chapter 2 and 3, the influence of past experience and the influence of processing visual target information on grasping behavior are explored in Chapter 4 and 5. I argue that, by storing information about target features in memory, movement planning and execution becomes more efficient and flexible. Electrophysiology as well as behavioral studies showed sustained cortical activity during the time from first seeing the target until acting towards it some moments later, suggesting that a representation of the movement plan is preserved for some time interval (Andersen & Buneo, 2002; Curtis & D'Esposito, 2003; Curtis & Lee, 2010; Hesse & Franz, 2009; Ikkai & Curtis, 2011). In Chapter 4, a pick-and-place paradigm with natural objects is used, where the location of the object and the object is varied from trial to trial, to examine intertrial priming effects on natural grasping behavior. Chapter 5 addresses the question concerning what features of an object have to be processed in order to generate the visuomotor priming effect?

Chapter 2: Salience map signals guide behavior in a motor-unspecific way

At some point in the brain, neuronal pathways for controlling attention, eye movements, and hand movements diverge. Salience maps are assumed to operate before the divergence of neuronal processing paths for attention and eye movements. The current question is, whether salience maps are also operative before the divergence of neuronal paths for hand movements or only thereafter. Several modulations of salience affect the speed of visual search for feature singletons: feature contrast, cross-trial dimension sequences, semantic pre-cueing of the target dimension, and dimensional target redundancy. If salience signals also guide manual pointing movements, they should be affected by the same manipulations of salience. In four experiments, visually-guided pointing movements were affected by feature contrast, cross-trial dimension sequences, semantic pre-cueing of the target dimension, and dimensional target redundancy. These results support the concept of a salience map that is motor-unspecific and is able to guide attention as well as eye and hand movements.

Chapter 3: Fitts' Law for salience and how the strength of pop out affects difficulty of reaching movements

Reaching movements increase in duration the more difficult the target is to reach as well described by Fitts' Law, which was mostly investigated by presenting only one target in isolation, not in cluttered scenes as in most everyday reaches. For 'pop-out' targets of different salience, we found the duration of observers' reaching movements to increase linearly with the logarithm of the target's salience, and Fitts' Law adapted for saliences accounted for nearly 90% of the variance in movement durations. Further, the influence of salience on movement durations was evident even when observers had sufficient time to select the target. Finally, movement durations were unaffected by target features if the target was presented in isolation, without any 'distractors'. We propose the integration of current theories of motor control with the concept of the salience map, thereby extending the perception-action framework from movement planning to movement execution.

Chapter 4: Feature-based intertrial effects in grasping are location unspecific

The preceding pick-and-place task influences the kinematics of a subsequently executed task. Both spatial properties as well as non-spatial properties of recent actions have been demonstrated to affect movement planning and execution on a given trial. An influence of non-spatial properties of recent experience has hitherto not been examined in an intertrial paradigm - that is, in the previous intertrial studies, only one of the two factors object location or object presence was variable across trials, at a time. We investigated whether intertrial priming effects of object features are location specific or can be generalized over changes of location. Participants grasped either a wine or a water glass from two different starting positions and placed it onto a box. The glass (wine or water) and the position of the glass (left or right from the resting position) were either the same or varied between trials. The results showed that repeating the same glass consecutively over two trials yields in faster movement planning and faster grasping movements independent of the position of the glass in the last trial. In contrast, repeating the starting position over two consecutive trials did not result in faster movement planning and grasping movements. Consequently, our results indicate that memory traces responsible for feature-based intertrial effects are not location specific, but can affect subsequent grasping movements even when they differ in spatial parameters.

Chapter 5: Visuomotor priming effects in grasping depend on the quality of cue processing

Visuomotor priming happens when viewing an object and results in internally simulated motor representations being facilitated for the object just observed compared to any other object. However, there continues a debate what factors are required for such priming effects to occur. In this chapter, the role of cue exposure time and quality of cue processing on visuomotor priming is investigated. Does simple exposure time have an impact on visuomotor priming effects or is rather the quality of cue processing the relevant factor. Natural objects (wine or water glass) were used as action and as cue objects in a pick-and-place task. The factor cue exposure time (short vs. long) was crossed with relevance of cue identity in a secondary memory task (relevant vs. irrelevant). Grasping of the target glass was faster when the cue was congruent to the target glass compared to when it was incongruent but only if the cue was relevant for the secondary task. No visuomotor priming effects occurred if the cue’s identity was irrelevant, irrespective of how long observers were exposed to the cue. The results suggest that visuomotor priming does not occur automatically by merely viewing objects, but the relevant feature of the cue object that can be congruent or incongruent, has to be task-relevant as well.

CHAPTER II

Salience map signals guide behavior in a motor-unspecific way[1]

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[1] A version of this chapter has been published as Zehetleitner, M., Hegenloh, M., & Müller, H. J. (2011). Visually guided pointing movements are driven by the salience map. *Journal of Vision, 11*, 24.

The basic theoretical concept of the salience map as well as psychophysical and neurophysiological evidence in favor of salience maps has been introduced in the *General Introduction*. An important feature of the salience map is its motor-unspecificity, meaning that signals from the salience map are able to guide not only covert attention, but also eye and limb movements (e.g., Gottlieb, Balan, Oristaglio, & Schneider, 2009). Empirical evidence regarding the motor-unspecificity comes from a number of different paradigms including yes/no detection, left/right localization, perceptual discrimination, as well as modulations of salience in eye and limb movements. However, a question still remains - what is the specific time course of selecting the first item in the search array?

The salience map is sometimes also named *priority map*, because of its ability to prioritize salient locations over non-salient locations. Thus, the salience map produces a map of selection probabilities for locations to be analyzed further. The assumption of the priority map has been investigated using a visual search paradigm. On the one hand, in an easy visual search task using feature singletons with, e.g., a red amongst green items, the target is selected very quickly and independently of the number of items in the search display (e.g., Treisman & Gelade, 1980; Wolfe, 1994). On the other hand, in a more difficult visual search task using spatial configurations with, e.g., a digital 2 among digital 5s, the target is usually selected much slower than in the singleton search and is highly dependent on the number of items in the display (e.g., Wolfe, Palmer, & Horowitz, 2010). These two basic findings from the visual search literature are explained in the following way using the concept of the salience map (e.g., Itti & Koch, 2000): a feature singleton is always the first item to be selected on the priority map and this is also the reason why adding more items to the visual search display does not affect search times. While searching for spatial configurations in a visual search display, the digital 2 does not produce a higher activation on the salience map than the other items in the display. Therefore, all items have to be selected and checked in a serial manner until finding the target. For this reason, adding items to the search display results in increased search times.

What happens to search behavior when the target item is always selected first but varies in saliency (e.g., luminance feature contrast)? A further increase in the salience of the target item results in faster search times (e.g., Found & Müller, 1996; Maljkovic & Nakayama, 1994; Verghese & Nakayama, 1994). This performance modulation stems from a faster deployment of attention towards the target and therefore affects the time course of selection.

Both the selection probability and the time course of selecting an item have been investigated by means of a number of paradigms, stimuli, and dependent variables. Selection probability has mostly been studied using saccadic eye movements as the preferred measure and natural images varying in salience (e.g., Bruce & Tsotsos, 2009; Seo & Milanfar, 2009). While the time course of selecting a target has been studied extensively using classical visual search paradigms with laboratory stimuli (e.g. bars or discs) and button-press responses (e.g., Found & Müller, 1996; Maljkovic & Nakayama, 1994; Verghese & Nakayama, 1994), there has been almost no study examining the time course of selecting an item using natural images. Only a small number of studies exist investigating the time course of selection in psychophysical stimuli using visually-guided saccades and pointing movements (e.g., Becker, 2008a, 2008b; Song & Nakayama, 2006). The reason why most research investigating the time course of visual selection has been done on manual key presses is based on the assumption that the salience map signals in a motor-unspecific way. This feature (i.e., motor-unspecificity) of the salience map predicts that the same salience signal affects covert attentional selection, saccadic eye movements as well as reaching movements. While the motor-unspecificity of the salience map is commonly accepted, there is almost no psychophysical evidence investigating this feature of the salience map. To better understand the motor-unspecificity assumption and to be able to generalize from simple button-press responses to more complex forms of action, more empirical evidence is needed.

Recently, the motor-unspecificity feature of the salience map received support from the neurophysiological level (Gottlieb, et al., 2009). Two theoretical possibilities for selecting a target for saccadic eye and limb movements were identified by Gottlieb et al. (2009). One possibility is based on the feature of the salience map previously described, that signals from the salience map and the corresponding location of the target coordinates can not only be used to guide attention but also eye and limb movements (see Figure 1). The other possibility is that the output of the salience map is motor-specific, meaning that the target selection is performed in the same area as the movement is performed (see also Gold & Shadlen, 2007).

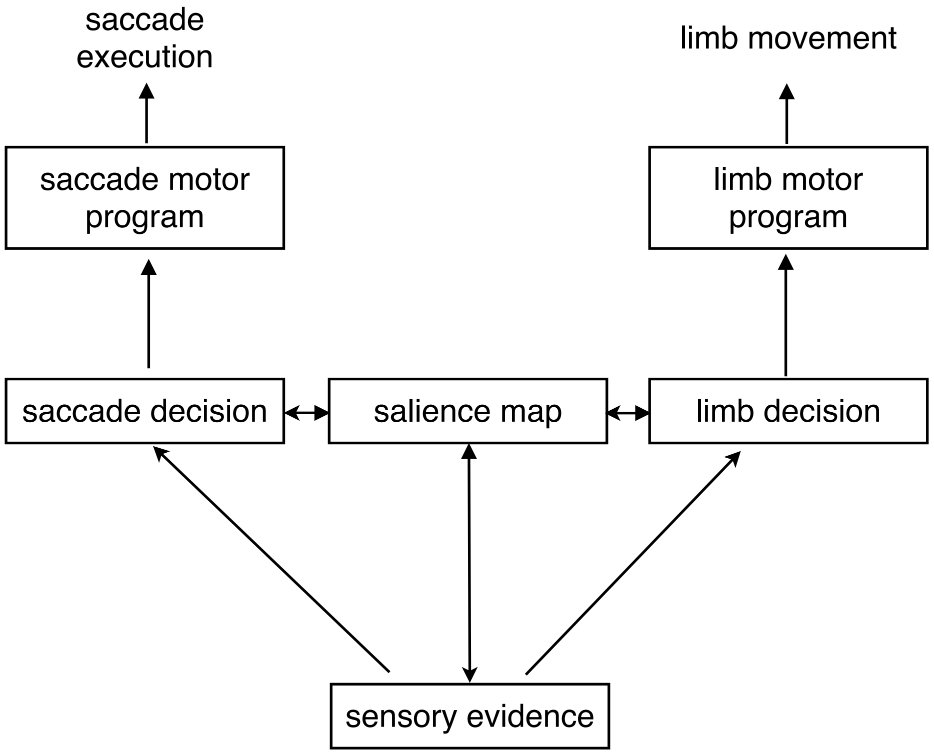

Figure 1. A processing architecture for saccades and limb movements illustrated with the concept of a motor-unspecific salience map with the ability to exchange information with both the perceptual stage and the motor decision stage (see Gottlieb et al., 2009, for a similar illustration).

The aim of Chapter 2 was to contribute to the still missing psychophysical evidence that signals from the salience map can be used independently of the action or in other words are motor-unspecific. Within the visual search literature, there are a number of well substantiated findings and effects that describe the time course of attentional selection dependent on variations in saliency of the target. As pointed out earlier in Chapter 2, these studies were conducted by participants pressing a key which is in contrast to the present chapter where participants perform a visually-guided pointing movement. If the predictions of the motor-unspecificity of the salience map are correct, then the same effects as in standard visual search tasks should also be observable in the initiation latency of visually-guided pointing movements, whereas not finding these effects would suggest a motor-specific modulation of the salience map.

Up to now, only a limited number of studies have investigated visual search behavior using manual pointing movements (e.g., Song & Nakayama, 2006, 2008, Song, Takahashi, & McPeek, 2008). The priming of pop-out (PoP) effect was investigated by Song and Nakayama (2006) using visually-guided pointing movements. In the PoP paradigm, participants have to search for an odd-colored diamond and report if the edge of the diamond was chipped of on the right or the left side. The crucial manipulation in the paradigm is the inversion of target and distracter color from trial to trial, e.g., in one trial all distracters are red and the target is green, while in the other trial the distracters are green and the target is red. RTs in the PoP task are found to be faster when the color assignment of the target and distracters stays the same across two consecutive trials compared to when the assignment changes and this effect has been named *intertrial priming.* In the study of Song and Nakayama (2006), participants had to point to the target as fast and accurately as possible, while the PoP paradigm was the same. They found pointing movements to be faster and more accurate the more items were present in the display and concluded from this finding that focal attention is necessary for visually-guided movements. Hence, this finding can support the claim that the salience map is indeed signaling in a motor-unspecific way, because the same effect was found in visual search tasks using button-presses or saccadic eye movement responses. Yet, display density in the search array has been reported to have an effect only in discrimination tasks and importantly not in detection tasks (e.g., Bravo & Nakayama, 1992), while detection tasks have been reported to be influenced by salience manipulations (e.g., Found & Müller, 1996; Nothdurft, 2002).

As pointed out in the present chapter, the evidence to support the notion of a motor-unspecific salience map is still weak and therefore needs to be examined with a range of well-known salience modulations in visual search tasks. The experiments in the present chapter thus investigated the following four classical visual search manipulations: (i) feature contrast, (ii) dimensional intertrial transitions, (iii) dimensional top-down cueing, and (iv) dimensional redundancy of target definitions. While manipulation (i) and (iv) influence only *bottom-up* saliency, manipulation (ii) and (iii) are not only influenced by bottom-up saliency factors.

By manipulating the feature contrast of target and distracter values, the strength of the salience signal is modulated (e.g., Bruce & Tsotsos, 2009; Wolfe & Horowitz, 2004). By making the target and distracter more similar, the salience signal of the target compared to the distracters is less strong. In visual search tasks, the time to find the target increases as the salience signal decreases (e.g., Sato, Murthy, Thompson, & Schall, 2001).

The second manipulation, dimensional intertrial transitions, has been found to influence search times in the following way: if the target-defining dimension (e.g., color or orientation) is different on trial *n* compared to trial *n-1*, search times increase compared to when the target-defining dimension is constant throughout two consecutive trials (e.g., Found & Müller, 1996). Recently, the underlying electrophysiological correlate of the dimensional intertrial transition has been identified in the N2pc event-related component (Töllner, Gramann, Müller, Kiss, & Eimer, 2008). The N2pc component has been tagged as a marker of attentional selection (e.g., Luck & Hillyard, 1994a). When repeating a trial with the same target-defining dimension, N2pc latencies are shorter compared to changes of the target-defining dimension (Töllner, et al., 2008). Dimensional weights therefore modulate basic salience computations.

In addition, dimensional weights can also be modulated in a top-down manner by instructing participants in the beginning of each trial to prepare for one target-defining dimension (e.g., Müller, et al., 2003). Behavioral as well as neurophysiological evidence shows that when participants receive a valid dimensional pre-cue before the trial, search times decrease and N2pc latencies are shorter (Töllner, Zehetleitner, Gramann, & Müller, 2010).

Lastly, as pointed out in the *General Introduction*, the master saliency map integrates signals from different dimensions (e.g., color, orientation). If a target is defined in *two* dimensions simultaneously, as compared to just one dimension, search times decrease (e.g., Krummenacher, Müller, & Heller, 2001, 2002). In addition, it was demonstrated that dimensional redundancy effects are based on co-activation (i.e., salience summation), instead of a parallel race, i.e., a parallel interactive processing or serial exhaustive processing of the different feature contrast signals (Zehetleitner, Krummenacher, & Müller, 2009). As in the last two visual search manipulations reported here, N2pc latencies were found to be shorter for dimensionally redundant target compared to targets just in a single dimension (Töllner, Zehetleitner, Krummenacher, & Müller, 2011).

To summarize, feature contrast, dimensional intertrial transitions, dimensional top-down cuing, as well as dimensional redundancy of target definitions have been found to modulate search times and therefore salience signals in classical singleton visual search tasks. The aim of Chapter 2 was to investigate these four manipulations in four experiments and how exactly these modulations influence movement initiation latencies in visually-guided pointing movements.

Specific motivation of the four experiments. In *Experiment 1*, the saliency signal was modulated by varying the feature contrast of the target item in two different dimensions (orientation and luminance) with five different levels of feature contrast in each dimension. As pointed out earlier, even if the target item is the first to be selected, by further increasing target salience, search becomes faster (e.g., Verghese & Nakayama, 1994; Zehetleitner, Proulx, & Müller, 2009). This further decrease in the time to find the target has been demonstrated by examining the slopes of different set size conditions (i.e., the number of items in the display) and finding that the slope remained close to zero, while the intercept changed with the salience manipulation (e.g., Zehetleitner, Krummenacher, & Müller, 2009). This has, however, only been demonstrated in detection paradigms and not in a paradigm using visually-guided pointing movements, which allows to draw conclusions about the motor-unspecificity of the salience map.

Experiment 2 was designed to examine dimensional intertrial transitions, that is to compare consecutive trials in which the target-defining dimension stayed constant versus trials in which the target-defining dimension changed. As in the previous experiments investigating dimensional intertrial transitions (e.g., Found & Müller, 1996; Töllner, et al., 2008), movement initiation latency in Experiment 2 was expected to be faster for trials of dimension repetitions compared to trials of dimension changes, due to the assumption that the salience map is motor-unspecific. The dimension repetition effect (DRE) is calculated as the difference in RT for trial n compared to trial n-1 for dimension repetitions versus dimension changes.

In *Experiment 3*, the top-down cueing of target dimensions was investigated by semantically pre-cueing the target dimension. Top-down pre-cueing effects have been found in yes/no detection (Müller, et al., 2003) as well as in perceptual discrimination tasks (Töllner, et al., 2010) and in Experiment 3, the dimension cueing effect (DCE) was expected to reveal faster initiation latency times in case of a valid pre-cue.

Experiment 4 aimed to investigate the effect of salience on visually-guided pointing movements by defining the target in a dimensionally redundant way. Several possible accounts exist for explaining why targets defined in a redundant manner are responded to faster than targets defined only in one dimension (redundant signals effect, RSE). One possibility was discovered by Raab (1962), who explained the RSE as a statistical facilitation in an independent parallel race of the two target-defining features in the redundant target. This facilitation is explained by a race between the two redundant signals until a response is executed. As the two signals have overlapping distribution of triggering a response, the chance that one signal reaches the boundary to trigger a response faster than the other is likely, hereby yielding to a RSE. From these two overlapping distributions, it is possible to determine an upper boundary (formalized by the race model inequality, RMI) of how large the RSE can get theoretically in a parallel independent race (Miller, 1982). Miller therefore proposed the co-activation model, which integrates both response-relevant signals before eventually triggering a response. Salience models (e.g., Bruce & Tsotsos, 2009; Itti & Koch, 2001) have been proposed in their architecture to work in a similar manner as the proposed co-activation model in which feature contrast signals from two dimension of the same location are being summed up on the master salience map to guide attention. Violations of the RMI have also been investigated and found in a number of visual search studies (e.g., Krummenacher, Müller, et al., 2001, 2002; Töllner, Zehetleitner, Krummenacher, et al., 2011). The RSE has been found to interact with feature contrast, in that the RSE was smaller for high-contrast targets compared to low-contrast targets, which ruled out the possibility that violations of the RMI could stem from serial-exhaustive models (Zehetleitner, Krummenacher, & Müller, 2009). If the salience map signals in a motor-unspecific manner, then violations of the RMI should also be visible in visually-guided pointing movements.

Methods

The following Methods part will cover all four experiments. Differences in stimuli and design between the four experiments are pointed out.

Participants. Overall 63 participants took part in all four experiments, were paid 8 € per hour and were naive to the hypotheses of the experiments. In Experiment 1, 12 participants were recruited (4 males; 2 left handed; with normal or corrected-to-normal vision; median age 25 years). In Experiment 2, 12 participants took part (5 males; all right handed; with normal or corrected-to-normal vision; median age 24 years). In Experiment 2, three participants were excluded from further analysis and replaced by additional participants, because the mean movement initiation latency was below 100 ms, while one observer was excluded because of an error rate above 15%. In Experiment 3, 13 participants were recruited (4 males; all right handed; with normal or corrected-to-normal vision; median age 24 years). In Experiment 4, 26 participants took part (11 males; one left handed; with normal or corrected-to-normal vision; median age 24 years). In Experiment 4, two participants were excluded from further analysis and replaced by additional participants, because the mean movement initiation latency was below 100 ms. A number of participants took part in all four experiments: 6 participants from Experiment 2 took part in Experiment 1; 4 participants from Experiment 3 took part in Experiment 1 and 2; and 4 participants from Experiment 4 took part in Experiment 1 to 3.

Apparatus. Stimuli were presented on an ELO 17” CRT Open-Frame (ELO Touch Systems, Elo Entuitive Systems, Fremont, CA) touchmonitor driven by a PC with Windows XP operating system. The CRT touchmonitor was mounted into a cut-out gap of a table, at an angle of about 30° to the surface of the table (see Figure 2a). The whole apparatus was placed in a sound-isolated chamber with a dim background light below the table. Participants were instructed to keep a viewing distance of 50 cm to the center of the monitor throughout the experiment. Participants were instructed to point as fast and accurately as possible with their index finger of their dominant hand to the feature singleton target in the visual search array on the monitor. The touchmonitor had a sensitive glass-layer converting pressure into electrical signals. By a company provided driver, the electrical signals were transformed into mouse-clicks, including the x-y coordinates on the screen. The mouse-click was then recorded by a recording software (written in C++). The apparatus was the same across Experiment 1 to Experiment 4.

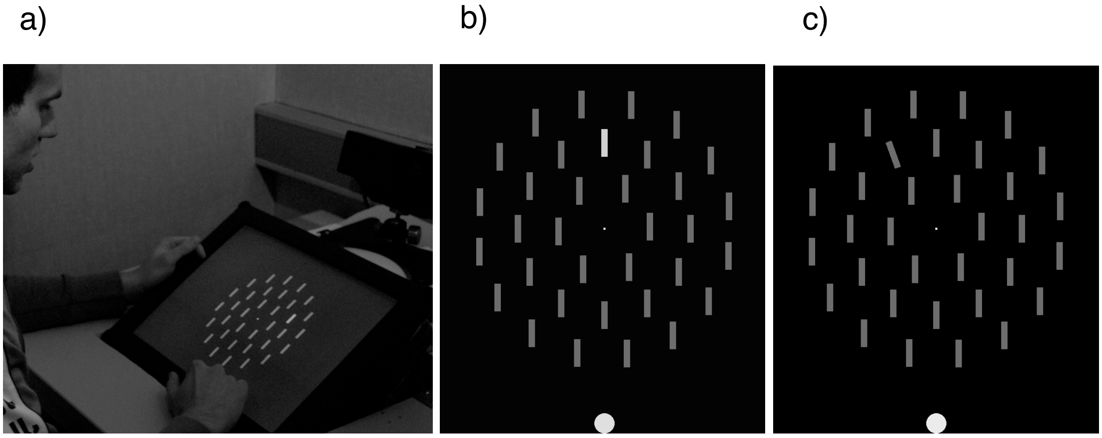

Figure 2. (a) Experimental setup for all experiments in Chapter 2 with an inbuilt touchscreen monitor. (b-c) Sample search displays with a luminance target (b) and an orientation target (c).

Stimuli and timing. The search display was made up of gray, upright rectangles (bars), each subtending 0.6° of visual angle wide and 2.7° high, and were arranged on three concentric (imaginary) circles around a white fixation point in the middle of the display on a black background (0.6 cd/m^2). There were six, twelve, and sixteen equidistant items placed on the three invisible circles with 4.5°, 8.5° and 12.5° in radius. A target was placed in a random way at one of the seven possible location on the upper half of the middle circle with each of these seven positions equally likely to contain a target (see Figure 2b and Figure 2c). In Experiment 1, the five levels of target orientation were used relative to the vertical distracters (0°). The target could be tilted to the right or to the left at each level, relative to the vertical distracters with orientation contrasts of 5°, 10°, 15°, 20° and 45°. Luminance targets were varied using a number of brightness levels (38, 19, 14, 13, and 10 cd/m^2) compared to the distracters (5.9 cd/m^2).[2] The stimuli in Experiment 2 and Experiment 3 were the same as in Experiment 1, except the targets with two orientation targets of 5° or 20° and two luminance targets with 21.1 and 10.4 cd/m^2 relative

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[2] In an additional control experiment with a go/no-go detection task, it was verified that even low-feature contrast targets were found in an efficient manner. The 95% confidence intervals of the search slopes ranged from -4.6 to 3.0 ms/item.

to the distracters. In Experiment 3, the only difference was the additional presentation of a semantic cue, which indicated the likely target-defining dimension of the upcoming trial. There were neutral and dimensional cues, with neutral cues providing no information about the upcoming target-defining dimension, while dimensional cue were 100% predictive about the upcoming target-defining dimension. The cues were presented on the monitor as German words with “SCHRAEG” for an orientation-defined target, “HELL” for a luminance-defined target, and “NEUTRAL” providing no information about the upcoming target. In Experiment 4, the stimuli were the same as in Experiment 2 and 3 with additional four redundant signal conditions, which were defined in both the luminance and orientation dimension, i.e., the target could be dim-shallow, dim-steep, bright-shallow and bright-steep. The target could be tilted equally often to the right or to the left of the vertical distracters and was randomized by the presentation software and not recorded (i.e., it was not possible to analyze for right/left orientation differences). A trial started with the simultaneous onset of the whole search array which remained visible until the response of the participants. The intertrial interval (ITI) was 900 ms with a temporal jitter of 200 ms. In Experiment 3, a trial started with a fixation dot for 900 ms, with a 1000 ms presentation of the dimensional or neutral cue followed, and finally another 900 ms fixation dot presentation until the search array onset. The amount of dimensional to neutral cues was 80% (equal number of luminance and orientation cues) to 20%. The first block in all four experiments was not analyzed as it was used for practice.

Design and procedure. Participants were instructed to point to the target with their index finger. After pointing to the target, the index finger had to be moved back to the central starting position at the lower end of the screen (marked by a grey disk with 1.5° in diameter). A new trial would only start after the index finger had been moved back to the starting position. After the last trial in each block, participants were informed about their average total time (i.e., initiation latency and movement duration) and error rate of the last block. In Experiment 3, participants were additionally instructed to actively set themselves for the upcoming target-defined dimension indicated by the cue. Experiment 1 consisted of one session lasting about 45 min with a total number of 1080 trials of 60 trial per block. Experiment 2 consisted of one session lasting about 45 min with a total number of 1140 trial of 60 trials per block. Experiment 3 consisted of one session lasting about 20 min with 240 trials of 60 trials per block. Experiment 4 consisted of two sessions of about 45 min each with 2592 trials, split into 72 trials per block.

Data analysis. Data analysis was performed using R (R Development Core Team, 2006). An error was defined as the landing position of the index finger deviating more than one degree of visual angle from the center of the target item. Initiation latency was defined as the interval between the onset of the search display and the onset of the movement. Movement duration was the interval between movement onset and movement offset (i.e., the touch on the display). The total time was defined as the sum of initiation latency and movement duration. Initiation latencies faster than 150 ms or total times exceeding 1800 ms were defined as outliers and not included in the analysis. The number of errors and outliers were less than 2%. Movement latency, movement duration, total times and error rates were analyzed by repeated-measures analyses of variance (ANOVAs) with the factors described for each experiment.

Results

The result section of Chapter 2 is divided into a separate section for each experiment and for each experiment initiation latency, total time, movement duration, and error rate are reported separately. ANOVA results are presented in tables for each experiment separately.

Experiment 1: varying levels feature-contrast

Initiation latency. Significant main effects were revealed for dimension and feature contrast, as well as a significant interaction between feature contrast and dimension (see Table 1 for detailed ANOVA results). Faster initiation latencies were obtained for high feature-contrast compared to low-feature contrast targets (407 vs. 440 ms), and targets defined in the orientation dimension were responded to faster than targets defined in the luminance dimension (417 vs. 429 ms). The interaction between feature contrast and dimension was the result of the chosen feature contrast levels, which did not match in the two dimensions.

Total time. The results pattern for the total time was the same as for the initiation latency. Total times were faster for for high feature-contrast compared to low-feature contrast targets (589 vs. 650 ms), and targets defined in the orientation dimension were responded to faster than targets defined in the luminance dimension (610 vs. 629 ms).

Movement duration. The results pattern for the movement duration was the same as for the initiation latency. Movement durations were faster for for high feature-contrast compared to low-feature contrast targets (182 vs. 211 ms), and targets defined in the orientation dimension were responded to faster than targets defined in the luminance dimension (192 vs. 200 ms).

Error rates. The overall performance was very good with only 0.8% of errors. Fewer errors were made for high feature-contrast compared to low-feature contrast targets (0.3 vs 1.1% errors). Additionally, fewer errors were made for targets defined in the orientation-dimension compared to targets defined in the luminance dimension (0.6 vs 0.9% errors).

Table 1: ANOVA results for Experiment 1 (all with 11 degrees of freedom)

Factor	F	p
	Total time	
dimension	22.99	.001
feature contrast	63.33	.001
feature contrast x dimension	33.61	.001
	Initiation latency	
dimension	10.49	.01
feature contrast	20.09	.001
feature contrast x dimension	19.67	.01
	Movement time	
dimension	16.05	.01
feature contrast	39.28	.001
feature contrast x dimension	13.87	.01
	Error rates	
dimension	5.58	.05
feature contrast	3.49	.1
feature contrast x dimension	2.59	.14

Experiment 2: dimensional intertrial transitions

Initiation latency. Significant main effects were revealed for dimension, feature contrast, and dimension transition (marginally significant) as well as a significant interaction between feature contrast and dimension (see Table 2 for detailed ANOVA results). Faster initiation latencies were obtained for high feature-contrast compared to low-feature contrast targets (440 vs. 471 ms), and targets defined in the orientation dimension were responded to faster than targets defined in the luminance dimension (453 vs. 459 ms). The DRE was greater than zero for low feature-contrast targets [6 ms; $t(11)=-2.39$, $p<.05$], but not greater than zero for high feature-contrast targets [1 ms; $t(11)=0.66$, $p=.53$].

Total time. The ANOVA revealed significant main effects for feature contrast and dimension transition as well as a significant interaction between feature contrast and dimension. Faster total times were obtained for high feature-contrast compared to low-feature contrast targets (670 vs. 742 ms), and faster total times were obtained when the target-defining dimension was repeated compared to when it changed across two consecutive trials (703 vs. 709 ms). The DRE was greater than zero for low feature-contrast targets [12 ms; $t(11)=-3.88$, $p<.01$], but not greater than zero for high feature-contrast targets [1 ms; $t(11)=0.30$, $p=.77$].

Movement duration. The same pattern of ANOVA results was obtained for the movement duration as for the total times. Faster movement durations were obtained for high feature-contrast compared to low-feature contrast targets (230 vs. 270 ms), and faster movement durations were obtained when the target-defining dimension was repeated compared to when it changed across two consecutive trials (248 vs. 252 ms). The DRE was greater than zero for low feature-contrast targets [6 ms; $t(11)=-2.86$, $p<.05$], but not greater than zero for high feature-contrast targets [1 ms; $t(11)=-0.85$, $p=.41$].

Error rates. The overall performance was very good with only 0.9% of errors. Fewer errors were made for high feature-contrast compared to low-feature contrast targets (0.2 vs 1.6% errors). The interaction between dimension and dimension transition was significant as well.

Table 2: ANOVA results for Experiment 2 & 3 (Exp. 2 with 11 and Exp. 3 with 12 degrees of freedom)

	Experiment 2 (dimension repetition)		Experiment 3 (dimension cue)	
Factor	F	p	F	p
	Total time			
dimension manipulation	11.72	.01	8.15	.05
feature contrast	40.91	.001	121.66	.001
feature contrast x dimension manipulation	8.67	.05	5.35	.05
	Initiation latency			
dimension manipulation	4.44	.06	10.22	.01
feature contrast	11.89	.01	69.79	.001
feature contrast x dimension manipulation	5.69	.05	3.57	.08
	Movement time			
dimension manipulation	8.59	.05	0.17	.69
feature contrast	15.04	.05	15.33	.01
feature contrast x dimension manipulation	7.83	.05	1.78	.21
	Error rates			
dimension manipulation	1.32	.27	0.23	.64
feature contrast	7.94	.05	5.39	.05
feature contrast x dimension manipulation	0.49	.5	0.51	.49

Experiment 3: dimensional pre-cueing

Initiation latency. Significant main effects were revealed for dimension, feature contrast, and cue validity, as well as an almost significant interaction between feature contrast and cue validity (see Table 2 for detailed ANOVA results). Faster initiation latencies were obtained for high feature-contrast compared to low-feature contrast targets (519 vs. 646 ms), and targets defined in the orientation dimension were responded to faster than targets defined in the luminance dimension (570 vs. 595 ms) and most important, valid cued targets were responded to faster than neutral cued targets (575 vs. 590 ms). The DCE was greater than zero for low feature-contrast targets [19 ms; *t*(11)=2.21, *p*<.05], but not greater than zero for high feature-contrast targets [6 ms; *t*(11)=1.07, *p*=.31].

Total time. The same pattern of ANOVA results was obtained for total time as for the initiation latency. Faster total times were obtained for high feature-contrast compared to low-feature contrast targets (736 vs. 890 ms), and targets defined in the orientation dimension were responded to faster than targets defined in the luminance dimension (802 vs. 824 ms), and valid cued targets were responded to faster than neutral cued targets (805 vs. 821 ms). The DCE was greater than zero for low feature-contrast targets [27 ms; *t*(11)=2.40, *p*<.05], but not greater than zero for high feature-contrast targets [2 ms; *t*(11)=0.41, *p*=.69].

Movement duration. Only the effect of feature contrast was significant with high feature-contrast targets responded to fast than to low-feature contrast targets (217 vs. 245 ms).

Error rates. The overall performance was very good with only 1.3% of errors. Less errors were made for high feature-contrast compared to low-feature contrast targets (0.5 vs 2.2% errors).

Experiment 4: dimensionally redundant targets

In this result section only the relevant effect are reported, namely (i) the analysis of redundant targets, (ii) the analysis of the RSE, and (iii) the analysis of violations of the RMI. Results for feature contrast of the target are not reported here, since in Experiment 4, the same singly defined targets were used as in Experiment 2 and 3. Overall error rates were again low with only 0.8% of errors. The ANOVA revealed only a significant effect of target type [*F*(1,25)=18.21, *p*<.001], i.e., less errors were made by participants for targets defined in both dimensions (0.4% of errors) than for targets defined in just a single dimension (1.2% of errors).

Redundant signal trials. The redundant signal trials (RST) were analyzed by a repeated measures ANOVA with the following factors: feature contrast of the orientation component (steep vs. shallow) of the redundant target and feature contrast of the luminance component (dim vs. bright) of the redundant target. ANOVA results revealed both main effects and the interaction to be significant in the total time, the initiation latency, and the movement time (see Table 3 for ANOVA results). Redundant targets composed of high feature contrast targets were responded to faster than low feature contrast targets in the orientation component, for total times (615 vs. 640 ms), initiation latency (412 vs. 431 ms), and for movement time (202 vs. 209 ms). For the luminance component, the same pattern was visible for the total time (620 vs. 635 ms), the initiation latency (417 vs. 426 ms), and for the movement time (203 vs. 209 ms). The interaction between the two levels of contrast is evidence that the cognitive processing architecture cannot depend on serial checking of the two dimensions (Townsend & Nozawa, 1995; see Zehetleitner, Krummenacher, Müller, 2009, for an elaboration of this argument).

RSE. The RSE was analyzed by means of an ANOVA with the factors orientation feature contrast (steep vs. shallow) and luminance feature contrast (bright vs. dim). For all movement components (total time, initiation latency, and movement time) both main effects and the interaction were significant (see Table 3 for ANOVA results), as well was the RSE greater than zero for all movement components [all $t > 2.18$, $p < .05$], with the exception of the “steep-dim” condition in the movement duration [$t(25)=1.45$, $p = .16$].

Table 3: ANOVA results for Experiment 4 (all with 25 degrees of freedom)

	RSTs		RSE	
Factor	F	p	F	p
	Total time			
orientation component	131.07	.001	63.16	.001
luminance component	66.96	.001	60.34	.001
orientation component x luminance component	43.04	.001	106.05	.001
	Initiation latency			
orientation component	53.64	.001	12.71	.01
luminance component	27.75	.001	12.91	.01
orientation component x luminance component	9.48	.01	35.91	.001
	Movement time			
orientation component	27.4	.001	73.71	.001
luminance component	24.72	.001	58.84	.001
orientation component x luminance component	21.3	.001	88.18	.001

Violations of the RMI. The RMI was only violated in the total time of the movement. When the feature contrast was low in both target dimensions (“dim-shallow”), the RMI was significantly violated in the .05 quantile [$t(25)= 2.00$, $p < .05$]; and with high contrast in the orientation and low contrast in the luminance (“dim-steep”), the RMI was significantly violated within the quantiles ranging from .05 and .10 [$t(25)> 2.02$, $p < .05$]. With these two observed RMI violations, parallel race models can be ruled out for visually-guided pointing movements. Violations of RMI are a conservative hint for co-activation effects, which can be interpreted within the current experiment as salience summation.

Discussion of Chapter 2

Summary of Experiment 1. The results of Experiment 1 showed that visually-guided pointing movements (both the initiation latency and the movement time) are faster for high - than for low-feature contrast targets. In terms of the salience map, high-feature contrast targets increase the salience signal and therefore allow for faster visually-guided pointing movements. Regarding the motor-unspecificity, it can be concluded that feature contrast impacts performance of visual search behavior, not only for key-presses, but also for visually-guided pointing movements.

Summary of Experiment 2. Experiment 2 was aimed to investigate the DRE in visually-guided pointing movements. DREs were found in the initiation latency, movement time, and total time for low-contrast targets, but not for high-contrast targets. Consequently, the DRE is not only visible in standard visual search tasks (detection and compound), but also in visually-guided pointing movements.

Summary of Experiment 3. When pre-cueing the upcoming target dimension, faster initiation latencies and total times were found compared to a neutral pre-cue. Dimensionally pre-cueing the upcoming target did not affect movement times, which may be due to the general smaller effects in the movement duration compared to initiation latency effects. The observed DCE indicate that visually-guided pointing movements are affected the same way as standard visual search tasks.

Summary of Experiment 4. Experiment 4 investigated redundant signal targets in visually-guided pointing movements. Significant redundancy gains were detected and were larger for low - than for high-feature contrast redundant targets. Additionally, significant violations of the RMI and a significant interaction were found between the two feature contrast components in redundant targets. This data pattern suggests that the feature contrast signals from the two dimension in the redundant target were integrated in a co-activation like manner, which rules out parallel or exhaustive serial search. That is, redundant signal targets and therefore modulations of salience induced by redundant targets are also visible in visually-guided pointing movements.

Control for eye movements. As in none of the above experiments in Chapter 2, eye movements were controlled it is possible that the observed effects stem from making saccadic eye movements. To exclude this possibility, a control experiment similar to Experiment 1 was carried out but participants' eye movements were controlled in order to assure the fixation on the fixation dot. Eight participants took part in this control experiment and were instructed the same way as in Experiment 1. In this control experiment only orientation defined targets were presented with a tilt to the left or right by 6° or 45°. In total, 336 trials were presented, in blocks of 84 trials (the first block was again considered as a practice block and not included in the analysis). In addition to the setup described in Experiment 1, eye movements were recorded using the SR Research Tower-Mount EyeLink 1000 (at a sampling rate of 1000 Hz; SR-Research, Ltd., Mississauga, Ontario, Canada) and a combined chin and forehead rest. Trials in the control experiment were excluded when the amplitudes of horizontal and vertical eye movements exceeded 2.5° from the fixation cross (4.9%), as well as were error trials excluded (12%). As in Experiment 1 in this chapter, the total time revealed the main effects of feature contrast to be significant [$F(1,7) = 13.24$, $p < .01$] with high-feature contrast targets to be responded to faster than low-feature contrast targets (710 vs. 733 ms). Similar results were found for the initiation latency for feature contrast [$F(1,7) = 9.16$, $p < .05$] with faster initiation latencies for high - compared to low-feature contrast targets (452 vs. 461 ms). For the movement duration, the main effect of feature contrast was marginally significant [$F(1,7) = 3.62$, $p < .1$], with short movement duration for high - compared to low-feature contrast targets (258 vs. 271 ms). The observed result pattern is qualitatively similar to the results of Experiment 1. Therefore, the influence of eye movements for the experiments in Chapter 2 does not seem systematically biased by eye movements.

Salience map signals are motor-unspecific. The aim of the designed experiments in Chapter 2 was to investigate whether influences of salience observed in standard visual search tasks can also be observed in visually-guided pointing movements. If the salience map and the underlying salience summation models (e.g., Itti & Koch, 2001) are able to signal not only for covert attention and saccadic eye movements (e.g., Gottlieb, et al., 2009), but also for visually guided pointing movements, then it can be assumed that the output of the salience map is available to any kind of output modality. In Chapter 2, the initiation latencies of visually-guided pointing movements were faster for high - compared to low-feature contrast targets, for cross-trial priming repetitions compared to changes, for valid dimensional pre-cues instead of just a neutral pre-cue, and for targets that were redundantly defined in two dimensions instead of just one dimension. These just mentioned effects are well known modulations in classical visual search pop-out paradigms and have hitherto not been investigated in visually-guided pointing movements. Therefore, it can be argued that the output of the salience map is available not only to covert attention and eye movements, but also to visually-guided pointing movements.

Returning to the neuronal architecture of the salience map, it was pointed out in Chapter 1 that there are a number of relevant areas in the brain representing features of the salience map. Neuronal activity in the LIP is known to transmit salience signals independently of the task and the effector used to respond to the target (Gottlieb, et al., 2009). In the manual response task in the Gottlieb et al. study, a monkey was trained to respond differently on the letter “E” or mirror “E” by releasing one of two bars. Although the task was carried out without making eye movements, the LIP was still active despite the decision involved a manual and not a saccadic response.

Additional neurophysiological evidence suggests that signals from the FEF do not only signal saccadic activity, but also signal visual salience independent of the motor output (Thompson & Bichot, 2005). In their study, signals from the FEF displayed the location of the target independently of the upcoming saccade location, differentiated between targets and non-targets also in cases of no saccadic eye movement, and discriminated between targets and non-targets independent of the time to initiate an eye movement.

The psychophysical data from the current chapter and the neurophysiological data reported here suggest that signals from the salience map are motor-unspecific and can guide not only covert attention and saccadic eye movements, but also visually-guided pointing movements.

Considerations for present debates in visual search. The results of Chapter 2 showed evidence that dimension-based attention is not only able to affect salience computations in covert attention tasks (e.g., Müller & Krummenacher, 2006), but also other output modalities like the motor system responsible for eye and limb movements. Currently, there are two alternative accounts (dual-route models and response-based accounts) competing against the dimension-weighting account, and both of them assume that DRE and DCE can only occur in detection paradigms. Even though dual-route models (e.g., Chan & Hayward, 2009; Karen Mortier, van Zoest, Meeter, & Theeuwes, 2010) and response-based accounts (e.g., Becker, 2008a, 2008b; Theeuwes, Reimann, & Mortier, 2006) are distinct in their way of explaining dimensional effects in detection tasks, the two accounts agree that dimension-based effects in visual search can only occur in detection tasks in contrast to localization tasks (e.g., the task in the current chapter). Dual-route models argue that the salience map is engaged in all visual search tasks except detection tasks. A special non-spatial detection module signals the presence of feature contrast for a given dimension, but importantly not the appropriate location of the signal (see also A. M. Treisman & Gelade, 1980). According to the dual-route models, dimension-weighting affects only these detection modules and not the salience computation. Therefore, in visual search tasks that require to localize the target to solve the task, DRE and DCE should not be visible. Response-based accounts argue that dimension-based effects are bound to mechanisms of response selection (e.g., Cohen & Shoup, 2000). According to their predictions, dimension-based effects can be observed when dimension repetitions coincide with response repetitions as it is the case in classic detection tasks, in contrast to for instance, localization tasks.

Both of the above presented models have been challenged by studies finding DRE (e.g., Müller & Krummenacher, 2006; Töllner, et al., 2010) and DCE (e.g., Müller & Krummenacher, 2006; Töllner, et al., 2010). The results of Chapter 2 add further evidence against both the dual-route and the response-based account. Both of these accounts would not have predicted the results found in the experiments in Chapter 2. The present data also suggest why some earlier studies did not find dimensional effects in localization (e.g., Chan & Hayward, 2009) or in saccadic compound tasks (Becker, 2008a, 2008b) - these studies used only high-feature contrast targets and, as seen in the present chapter, dimensional effects in high-feature contrast targets were barely visible compared to the dimensional effects in low-feature contrast targets.

Recently, it has been shown in several paradigms that salience-based effects are larger for low- as compared to high-feature contrast targets. In a go/no-go detection task, redundancy gains were larger for low-feature contrast targets (Zehetleitner, Krummenacher, & Müller, 2009). DRE revealed the same pattern of results, with larger effects for low- as compared to high-feature contrast targets. In a left/right localization task, DRE as well as DCE were evident for low-feature contrast targets, but not for high-feature contrast targets (Zehetleitner, Krummenacher, Geyer, Hegenloh, & Müller, 2010). To sum up, salience-based effects such as redundancy gains, the DRE and the DCE were found to be larger in size for low-feature contrast targets as compared to high-feature contrast targets in localization, detection and visually-guided pointing tasks.

This described pattern of results was recently applied to the Ratcliff Diffusion Model (RDM; Ratcliff, 1978) logic onto visual search behavior (Zehetleitner & Müller, 2010). The RDM explains that stimulus quality differences are responsible for differences in decision times. These differences increase with a prolonged decision time (see also R. Ratcliff, Thapar, & McKoon, 2003). With regard to the results from the present chapter, larger effects were found throughout all experiments in the present chapter for low-feature contrast targets as compared to high-feature contrast targets. To resume the previous assumption why dimensional redundancy gains, DREs, and DCEs are detectable for high-feature contrast targets in detection paradigms, but not in localization, pointing or compound tasks, a computational model proposed by Zehetleitner and Müller (2010) argued that decision times were faster for localization than for detection tasks. And as seen in the present chapter, faster decisions as for the high-feature contrast targets lead to smaller salience-based effects.

In sum, the results of Chapter 2 show that initiation latencies of visually-guided pointing movements were faster for high- as compared to low-feature contrast targets, for cross-trial repetitions as compared to changes of the target-defining dimension, for valid dimensional pre-cues as compared to neutral pre-cues, and for redundantly defined targets as compared to targets defined in just one dimension. These results demonstrate that salience maps provide signals in a motor-unspecific manner and are not only able to guide attention and saccadic eye movements, but also visually-guided pointing movements.

CHAPTER III

Fitts' Law for salience and how the strength of pop out affects difficulty of reaching movements

In the present chapter the focus is on movement execution, which is defined as the process of the movement, when the hand is moving, in contrast to the process of movement preparation (see Chapter 2). In Chapter 3, the movement execution stage of the action is targeted in a series of experiments by manipulating the feature contrast of the target. The more difficult a movement is, the longer it takes for the movement to be carried out. This relationship has been first observed and quantified by Fitts (Fitts, 1954) and has lead to a lively discussion in the literature.[3] The basic finding is that for pointing movements to a target, the movement duration increases as the distance between initial position and target increases, and as the size of the target decreases. This relationship between movement duration and target distance and width obeys a well-defined quantitative relationship:

$$MD = a + b \log (2A) + c \log (1/W),$$

where MD denotes the movement duration, A the amplitude of the movement, W the width of the target area, and log is the binary logarithm (MacKenzie, 1989). The parameters *a*, *b*, and *c* depend on the effector type (e.g., pointing with the index finger, a mouse, or a pen) and variations of the basic paradigm (see Beamish et al., 2009 for a review).

Strikingly, in studies investigating Fitts' Law, there usually was one movement target presented in isolation, whose properties (location and size) were manipulated experimentally. However, most everyday reaching targets are embedded in cluttered visual and haptic environments (Meegan & Tipper, 1998), adding to the movement's difficulty. The difficulty or ease with which an object is discerned in, or singled out from, the visual scene has been examined in numerous studies mostly based on the visual search paradigm (Treisman, 1988; Wolfe, Cave, & Franzel, 1989). Specifically, a red apple can be visually differentiated in a crate of green apples more easily than an apple of yellowish-

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[3] Approx. 900 articles citing (Fitts, 1954); from a ISI Web of Knowledge query in July 2011.

greenish color (Duncan & Humphreys, 1989; Wolfe & Horowitz, 2004). How easily a location in a visual scene can be singled out from amongst the other locations is usually conceptualized in terms of a salience map, which quantifies how different each location is in terms of edge orientation, color, or luminance is from its surround (Koch & Ullman, 1985). At present, numerous algorithms exist for analyzing the salience of image locations (Bruce & Tsotsos, 2009; Itti & Koch, 2000, 2001; Li, 2002; Philiastides, Ratcliff, & Sajda, 2006; Walther & Koch, 2006).

Central to the current chapter is the linkage between perception and action (Bach, Gunter, Knoblich, Prinz, & Friederici, 2009; Rizzolatti, Riggio, Dascola, & Umiltá, 1987). The influential pre-motor account (Rizzolatti, et al., 1987) proposes a strong coupling between spatial attention and the programming of actions, in that attentional selection of a spatial location is synonymous with the setting-up of a motor plan to that location. Indeed, numerous psychophysical and neurophysiological studies have reported enhanced perception at locations to which actions (eye or hand movements) are planned and about to be executed (Baldauf & Deubel, 2010; Deubel & Schneider, 1996; Moore & Armstrong, 2003; Sheliga, Riggio, & Rizzolatti, 1995), and also that motor readiness increases for regions that are spatially attended (e.g., Craighero, Fadiga, Rizzolatti, & Umilta, 1999). Furthermore, for relatively cluttered scenes, it has been demonstrated that salience affects not only visual selection time (Zwickel, Grosjean, & Prinz, 2007) but also motor planning (Bach, et al., 2009; Rizzolatti, et al., 1987): in Chapter 2, movement initiation latencies were found to be shorter for targets of higher saliency and becoming gradually slower by reducing the feature contrast of the target with respect to the distracters. However, Fitts' Law (Fitts, 1954) describes how movement duration is related to the difficulty of the movement, that is, an effect originating from the stage of motor execution, rather than from motor planning. Since pre-motor theory (Bach, et al., 2009; Rizzolatti, et al., 1987), as it stands, make no statements about motor execution, it remains an open issue whether visual salience affects not only the planning, but also the execution of movements. Specifically, there are three unanswered questions as to the role of salience-dependent processes in Fitts' Law for movement durations: (i) Most fundamentally, is there a salience-dependent modulation of MDs (rather than just of initiation latencies); that is, are MDs influenced, in a logarithmic fashion, by a combination of both movement distance and target salience? (ii) If so, does the slowing of MDs with less salient targets originate from the motor planning or execution phases of the movement, rather than from visual selection of the target in a realistic (i.e., cluttered) cluttered scene? (iii) And is it indeed the local feature contrast of the target relative to its surrounding stimuli (i.e., its salience), rather than the target feature itself, that is responsible for the modulation?

Experiment 1

To examine the Fitts' Law relationship for more realistic, that is, relatively cluttered scenes, we collected data in three experiments. In Experiment 1, participants performed a visual search pointing task, looking for a tilted grey target bar among vertical grey distractor bars. While it was ensured that all targets 'popped out' of the scene (i.e., target detection times were independent of the number of distractors), the speed of pop-out was influenced by target salience (in terms of an intercept effect on the function relating detection time to distractor number). In all three experiments, participants initially fixated the center of the screen, with their right-hand index finger placed at a starting point below the fixation marker, which varied in distance to potential target locations. The task was to touch the target with this finger as fast as possible following the onset of the search display. Experiment 1 was designed to establish a basic effect of target salience on MDs proper, and whether taking salience into account would improve the Fitts' Law fit.

Method

Participants. 11 observers participated (4 male; all right-handed; all with normal or corrected-to-normal vision; median age of 25 years) in a 40-minute experimental session for payment (8 €, equivalent to USD 11, per hour).

Apparatus. Stimuli were presented on an ELO (ELO Touch Systems, Elo Entuitive Systems, Fremont, CA) CRT Open-Frame 17” touch monitor driven by a personal computer (PC, Windows XP operating system). Participants responded with the index finger of their dominant hand, pointing as rapidly as possible to a feature singleton target. At the end of each block of trials, participants were informed about their mean total movement time achieved in the block.

Stimuli and Timing. The display consisted of grey, upright rectangles (bars) that were arranged on three concentric (imaginary) circles, of radius 4.5°, 8.5°, and 12.5° of visual angle, respectively, around a white fixation point on a black background (of luminance 0.4 cd/m^2). There were six, twelve, or 16 equidistant locations on the small, medium, and large circle, respectively, where the stimuli were placed. Each bar was 0.6° wide and 2.7° high. One target was randomly placed at one of the seven possible positions on the middle upper (semi-) circle. These were arranged with a vertical and horizontal distance between each other of approximately 1.6°, with a jitter of about 0.2°. Orientation targets could differ from the vertical distracters by a tilt to the left or the right of 4°, 6°, 10°, 20°, or 45° respectively. In a pilot experiment, we examined the search efficiency for the above target (and distractor) specifications by systematically varying the set size in a simple target detection task. Detection reaction times did not increase significantly with set size. The confidence intervals of the slopes of the functions relating reaction time to set size all included zero, indicating that all the targets used in the present chapter do ‘pop out’ from the display.

Three different starting positions were introduced for the pointing movements, to vary their amplitudes to the target: the staring positions had a distance of 14, 18, and 22 cm, respectively, from the fixation point in the center of the display. The starting positions varied from block to block.

Design and Procedure. Participants were instructed to use their dominant index finger to point to the target and then to move the index finger back to the same starting position at the bottom of the screen (a trial would be initiated only if the observer touched the starting position). Participants were told to keep their index finger on the starting position until they had localized the target and only then lift the finger and point to the target as fast as possible.

Data Analysis. Data analysis was implemented using R (R Development Core Team, 2011). An error was defined when the landing position of the finger deviated by more than 1° of visual angle from the center of the target. Initiation latency was defined as the interval between stimulus and movement onset. Movement duration was the interval between movement onset and offset. Total time was the sum of initiation latency and movement duration. Trials on which latencies were below 150 ms or total times were above 1800 ms were excluded as anticipatory movements and outliers, respectively. Less than 1.5% of the trials were excluded because of errors, latency, or total times criteria.

Results

Movement durations (MDs; i.e., the time post display onset from lifting the finger off the starting position to touching the target on the screen) increased with increasing distance of starting point from the target; additionally, MDs increased with decreasing feature contrast (see Figure 1a). Standard Fitts' Law relates MDs to the natural logarithm of distance (D) divided by the required landing point precision, that is: the larger the movement distance and/or the higher the required precision, the longer the movement takes. Given that precision was constant in the present experiments, mean MDs (averaged over participants) were subjected to a linear regression analysis according to the standard Fitts' Law: $MD=b_1*\log (D)$, as well as Fitts' Law including feature contrast (FC): $MD=b_1*\log (D)+b_2*\log (1/FC)$, where b_1 and b_2 are the free parameters of the model(s). Both models were compared using the Bayesian information criterion (Schwarz, 1978) in order to ascertain that any improvement in fit was not simply attributable to the addition of a free parameter. The Bayesian information criterion was lower for the model that included salience, compared to the standard model (132 vs. 148, see Table 1). The standard Fitts' Law regression model explained 60% of the variance in MDs, inclusion of feature contrast raised this to 88%.

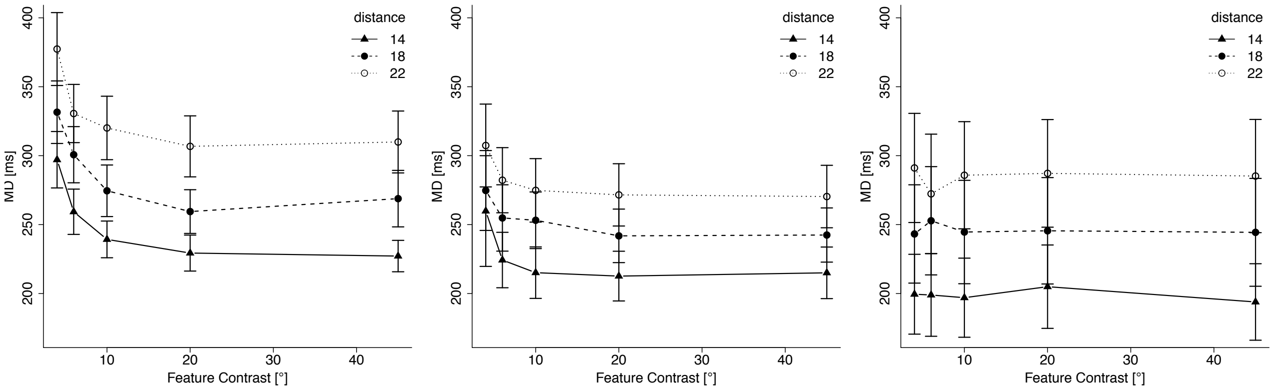

Figure 1 presents movement durations for all three experiments depending on feature contrast of the orientation pop-out target and movement distance.

An ANOVA of the movement errors, with the factors feature contrast and distance, revealed the error rates to be unaffected by distance (main effect of distance and feature contrast x distance interaction: *F*s<1, *p*s>.36), but to decrease with increasing feature contrast (*F*(4,40)=16.1, *p*<.001). Error rates were 6% for the 4°, 0.6% for the 6°, and zero for all higher orientation contrast conditions. The fact that the movements became not only faster, but also more accurate with increasing feature contrast rules out that the shortening of MDs is attributable to a speed-accuracy trade-off (SAT). Interestingly, on nearly all error trials, the landing point of the movement was close to a non-target position that could potentially contain a target (86% of the landing points on error trials were within the range of alternative target positions).

Furthermore, movement latencies (i.e., the time from display onset to movement onset) were little affected by distance [main effect: $F(1,10)=3.4$, $p<.09$], but increased with decreasing feature contrast [$F(4,40)=16.9$, $p<.0001$], from 419 ms with the highest to 584 ms with the lowest feature contrast.

Table 1. Explained variance of MDs and (in brackets) BIC values for all three experiments and the two different regression models, standard Fitts' Law and Fitts' Law with an additional feature contrast term.

Experiment	MD=a*log(D)+b	MD=a*log(D)+b*log(1/FC)+c
One	.60 (148.5)	.88 (132.3)
Two	.68 (131.3)	.88 (118.7)
Three	.98 (96.9)	.98 (99.4)

Taken together, movements were both initiated slower and took more time to execute (after initiation) for pop-out targets of low, as compared to high, salience. It is possible that the slowing of MDs with decreasing target salience is not due to motor processing, but rather to attentional-selection processes: Observers may have had to slow MDs for low-feature-contrast targets because selection had not been completed by the start of the movement and the precise landing position had to be calculated after the hand had actually left the starting position.

Experiment 2

In Experiment 2, participants performed the same visual search pointing task as in Experiment 1, the difference being that participants were not allowed to initiate the movements until after a delay of 1 s following display onset. This was meant to ensure that they had enough time to select the target and plan the movement before starting its execution, further isolating an effect of salience on MDs proper.

Method

Participants. 16 observers participated (4 male; all right-handed; all with normal or corrected-to-normal vision; median age of 25 years) in a 15-minute experimental session for payment (8 €, equivalent to USD 11, per hour).

Apparatus, Stimuli, and Design. The apparatus, stimuli and timing, and design were the same as in Experiment 1.

Procedure. In Experiment 2, observers were instructed to start the reaching movement not earlier than 1 second after display onset. This is in contrast to Experiment 1, where observers were to start moving their finger as soon as they had located the target. In an initial practice block of trials, observers were provided with an auditory feedback signal when they initiated the movement too early; the instruction was successful: the fastest movement latencies (0.1 quantile of the latency distribution) in Experiment 2 were 200 ms slower slower than the slowest latencies (0.9 quantile) in Experiment 1. Error trials were excluded from further analysis.

Results

As in Experiment 1, MDs were found to depend on both distance and feature contrast (see Figure 1b), and the regression of Fitts' Law including the feature contrast term accounted for 88% of the variance, which is greater than the 68% explained by the standard Fitts' Law (as indicated by a lower BIC value for the model including feature contrast; see Table 1). Thus, Experiment 2 demonstrates that salience still influences MDs even after the process of target selection is completed.

Experiment 3

In Experiment 3, participants performed the visual search pointing task without the display containing any distractors (in contrast to Experiments 1 and 2 where distractors were present). Given that the target bar was presented in isolation, its contrast to the background was effectively the same, whatever its orientation. This permitted effects of salience (Experiments 1 and 2) to be separated from those of the target feature itself (Experiment 3).

Method

Participants. 8 observers participated (4 male; all right-handed; all with normal or corrected-to-normal vision; median age of 25 years) in a 40-minute experimental session for payment (8 €, equivalent to USD 11, per hour).

Apparatus. The apparatus, and the design and procedure were the same as in Experiment 1.

Stimuli. The only difference to the stimuli used in Experiment 1 was that in Experiment 3, the target was always the only item in the visual display, i.e., distractors were not presented.

Results

If the MD effects related to salience in Experiments 1 and 2 were due to the visual features of the target as such, rather than its feature contrast relative to the surrounding distractors, the same relationship between target orientation and MD should be observed as in the previous experiments. However, as expected, this was not the case: only distance affected MDs, and the standard Fitts' Law explained 98% of the variance in MDs; adding the feature contrast term did not yield a significant increase (lowest BIC for the standard Fitts' Law model, see Table 1). Error rates were zero for all conditions.

Discussion of Chapter 3

Taken together, the data of Experiments 1 to 3 in Chapter 3 demonstrate that visual salience (feature contrast) affects the durations of reaching movements according to Fitts' Law (Fitts, 1954): the less salient the target becomes, the longer the movement takes to be completed.

Relation to models of Fitts' Law

How do the present data fit with existing accounts of Fitts' Law? Fitts' classical cognitive approach assumed that the information (measured in bits) required to specify the motor command for a particular movement increases with the movement distance to be covered and the required landing point precision. At the same time, the capacity to process, or transmit, motor commands is limited (fixed-capacity channel), so that the time required for signal transmission depends on the amount of information to be transferred: the greater the amount, the longer it takes to be transmitted. Consequently, increasing the amplitude or accuracy requirements of a movement increases the movement duration (Fitts, 1954). To explain the present findings within this cognitive framework, one would have to assume additionally that decreasing the salience of a target increases the size of the motor command (in bits), which – due to the capacity limitation in motor processing – leads to slowed MDs. In other words, the difficulty of a movement is not only a function of its amplitude and the required precision, but also of the salience of the target. Conceivably, for locations of higher salience, the spatial area indicated demarcated by the salience signal is smaller than that for locations of lower salience. A spatially more confined signal would be equivalent to less uncertainty about the target location, resulting in a smaller amount of information required for the motor command to specify the end point of the movement.

However, besides this cognitive approach, there are neurobiological models of motor control according to which Fitts' Law emerges from the inherent model dynamics, for both closed-loop (Beamish, et al., 2009) and open-loop circuits (Harris & Wolpert, 1998). Physiologically, motor noise is assumed to be signal-dependent, that is, as the size of a motor command (in terms of motor-neuron firing rates) increases, its variability increases too, resulting in a wider distribution (or reduced precision) of landing points (Harris & Wolpert, 1998; Todorov & Jordan, 2002). Consequently, for movements of greater amplitude or finer precision, the size of the motor commands has to be reduced, leading to slower movements. In the context of such models, the present findings would imply that targets of lesser salience have to be reached by implementing smaller motor commands (i.e., slower movements) in order to maintain precision, thus prolonging the MDs.

Representation of the landing position plays different roles for open- and, respectively, closed-loop control. In open-loop control, the landing position is specified at the beginning of the movement and not further ‘referred to’ during movement execution. Given this, it is difficult to conceive of how a decrease of the representational quality of the landing position caused by a decrease in target salience could be compensated for by slower movements. By contrast, in closed-loop control, where the estimated location of the effector is constantly compared to the intended landing position, a degraded representation of the landing positions (associated with reduced target saliency) may well be compensated for by slower movements.

Models of concurrent motor plans

There is one additional class of motor control models that explains why a reduction in salience results in slower movements: models of concurrent motor controllers, which have been proposed for reaching movements (Cisek, 2007; Tipper, Lortie, & Baylis, 1992; Wolpert & Kawato, 1998). According to the affordance competition hypothesis (Cisek, 2007), all sensory information that is processed in parallel by the visual system is used for the planning of potential actions. The resulting action plans are competing against each other for processing capacity in order to be actually carried out. Sensory information is sampled in an ongoing manner to bias the competition until a motor response is executed. Importantly for the question at issue, according to Cisek (Cisek, 2007), this competition continues during overt movements, and this chapter suggests that salience biases this competition: the more salient the target is relative to the distractors, the less the distractors compete with the motor plan directed at the target. This concept of multiple motor plans has been formally implemented for limb movements (see Meeter, van der Stigchel, & Theeuwes, 2010 for an implementation of this concept for eye movements). For limb movements, Wolpert and Kawato (1998) proposed a motor control model with multiple paired forward and inverse models, which is capable of adjusting several motor programs for a given environment. Crucial in this model is that both feed-forward and feed-back sensory signals are integrated into the currently executed motor program, making it possible for distractor locations to influence the trajectory of an ongoing movement. Related to reaches in cluttered scenes, there exists a motor plan for each object location in the display, and the strength of this plan is proportional to the salience of that location. In order to explain the present findings, this model has to be extended by assuming that during ongoing motor execution, interference from competing motor plans is proportional to the speed of the movement: the faster the movement, the greater the effect of interference. This assumption is plausible because at some point in time, the competition between salient targets and non-salient distractors is resolved. From then on, the only motor plan, which influences the ongoing movement, is that for the target position. Consequently, the slower the movement is executed, the higher the proportion of time during which the pure target plan drives the movement.

With this novel addition, the linking of salience models and models of concurrent motor plans can readily explain the demonstrated effects of salience on the movement durations, latencies, and accuracy of reaching movements in cluttered scenes: The more salient the target is compared to the distractors, the faster the target plan wins the competition for initialization (resulting in faster latencies). Additionally, the movement itself can be executed faster and more accurately because there is less ongoing interference during the execution of the movement (resulting in shorter durations). Conversely, when the target is less salient, it takes longer for the target plan to win the competition for initialization, and the movement has to be carried out more slowly in order to compensate for the continuing competition during movement execution. Importantly, salience has to be understood here as segregating figures from other figures, rather than figure from ground: when there is only one item in the display, as was the case in Experiment 3, only one motor plan is generated, i.e., there are no other motor plans that could interfere.

Salience and motor control

In summary, we have demonstrated that salience plays an important role in motor control when reaching for targets in cluttered scenes: the more salient the target is, the faster the movement can be initialized, the less time the movement takes to be executed, and the more precise the movement becomes. In the present chapter, salience was maintained at a level high enough for targets to ‘pop out’ from the cluttered scene (Treisman & Gelade, 1980), i.e., our manipulation of salience modulated the speed with which the target was attentionally selected, while maintaining a constant probability of 1.0 that the target was selected first, spatially in parallel (Töllner, Zehetleitner, Gramann, & Müller, 2011; Zehetleitner, Krummenacher, & Müller, 2009). Thus, the slowing of MDs caused by reduced salience of pop-out targets originates from the specification and execution of motor plans, rather than from difficulties in attentionally singling out the target from among the distractors. Extending Fitts’ Law to salience allows us to explain nearly 90% of the variance in observed movement durations. This Fitts’-Law-of-Salience effect can plausibly be accounted for by models of concurrent motor plans, according to which a motor plan is prepared for each (potential target) object in the scene. Motor plans compete against each other biased by object salience, and this competition continues to influence the ongoing movement until it is resolved. Consequently, slower movements lead to increased accuracy because a greater proportion of the movement is governed by a control signal that is no longer subject to competing influences from (more or less salient) distractors. Arguably, therefore, computational models of salience (Bruce & Tsotsos, 2009; Gao, Mahadevan, & Vasconcelos, 2008; Itti & Koch, 2001) and of motor control (Beamish, et al., 2009; Meeter, et al., 2010; Wolpert & Kawato, 1998) will have to be combined in the future to fully explain visually guided motor behavior. While in Chapter 2 and 3, the influence of salience maps on movement planning and movement execution was investigated, i.e., how perception and previous actions influence visually-guided pointing movements. Chapter 4 and Chapter 5 address the question, to what extent natural pick-and-place movements are influenced by previous actions (Chapter 4) or by what was previously perceived (Chapter 5).

CHAPTER IV

Feature-based intertrial effects in grasping are location unspecific

For humans to be able to grasp an object within reachable space, the motor system requires information about the object's position, size, and other features, which is provided by the visual system (Jeannerod, 1981, 1984). On a prominent view of the visual system (introduced in Chapter 1; Goodale & Milner, 1992; Milner & Goodale, 2006), following entry-level coding in the primary visual (occipital) cortex, visual processing fractionates, anatomically and functionally, into two separable systems: a ventral (occipito-temporal) stream involved in object identification and a dorsal (occipito-parietal) stream involved exclusively in motor programming. Despite the extensive work carried out over the past two decades to elaborate this "two-visual-systems hypothesis", a number of issues are still subject to debate. In particular, the neuroanatomical dissociation between the two systems is not quite as clear-cut as some proponents of this hypothesis would have it (see Gorea & Cardoso-Leite, 2010, for a review), and their functional dissociation is likewise not as clear as previously assumed (e.g., Farivar, 2009; Schenk & McIntosh, 2010). For instance, rather than the dorsal and ventral streams being two streams completely separated anatomically, third-order motion perception requires linkages between the two systems (Ho, 1998), likely involving visual areas V5 (dorsal stream) and V4 (ventral stream).

More pertinent to the question at issue in the present chapter, there is also a debate about how motor programs are formed within the two-visual-systems framework. Concerning this question, a "real-time view" of motor programming has recently been proposed (Westwood & Goodale, 2003, 2011), according to which the ventral system provides information about the identification of an object (information about form, color and pattern of the object are processed and coded in an allocentric way, i.e., scene-based coordinates and relational metrics; further referred to as ventral features), while the movement parameters proper (e.g., egocentric position of the target object) are only computed by the dorsal system (further referred to as dorsal features) when actually performing a target-directed action. So what aspects of a movement are affected by ventral vs. dorsal features? According to Westwood and Goodale (2003, 2011) dorsal features guide a grasping movement, but do not produce perceptual awareness of the object to be grasped. Ventral features create a perceptual representation of the target that can be stored in and accessed from memory and are only needed when the target is not visible during the movement. Consequently, on this view, any movement that is executed from memory (e.g., when the target object is not visible during movement execution) has to rely exclusively on ventral features, without the availability of target information provided by dorsal features. In contrast, movement programs computed by dorsal features that are required for precise, and fast grasping movements have no memory (Goodale, Jakobson, & Keillor, 1994; Milner & Goodale, 2006). If there is a delay between seeing the target and actually grasping the target, the grasping movement cannot be executed accurately, since ventral features have to be used to generate the movement program from memory (Westwood & Goodale, 2003).

Additionally, the real-time view of motor planning is a-historic in the sense that on a given trial *n*, any properties (e.g., location, size, or form) of a previously perceived and responded-to object (e.g., the object on the preceding trial *n-1*) should have no effect on how the movement to the current target is executed, because the exact movement parameters (e.g., target location, grip aperture, grip orientation) are computed by the dorsal stream in real-time for the current object. For the same reason, any action performed on the previous trial *n*-1 should also be incapable of affecting the motor plan on trial *n*.

However, recent studies found grasping movements to be influenced by preceding perceptual or motor events (Hesse, de Grave, Franz, Brenner, & Smeets, 2008; Jax & Rosenbaum, 2009), challenging the assumption of the a-historic, real-time specification of motor plans. With respect to preceding perceptual events, Hesse et al. (2008) asked their participants to grasp a cylindrical object tilted to the left or the right. Two seconds before action onset, participants were presented with a task-irrelevant ('cue') cylinder for a duration of 500 ms, which could have either the same, or a different orientation than the target. Hesse et al. found the instructed movement to be initiated faster when the target and cue objects were congruent, rather than incongruent, in orientation (same vs. different orientation). Additionally, grip orientation, too, was affected by congruency: following incongruent cues, the grip was oriented away from the target orientation from the time between reaching the maximum grip aperture (the distance between index finger and thumb during the grasping movement) and the time at which the target was actually lifted. This study showed that viewing a task-irrelevant cue two seconds before the response to the target still influenced non-spatial features of the current movement (dorsal features) and thus contradicting the real-time view.

With respect to spatial properties in intertrial action history, Chapman et al. (2010) instructed participants to perform a rapid reaching task to one of two possible targets. Crucially, the target location was not known until just after movement onset. That is, participants were forced to plan and initiate their movement without the exact location parameters being available. Chapman et al. found that the initial reach trajectories on a given trial *n* were shifted in the direction of the location of the target on the previous trial *n-1*; for instance, when the target on trial *n-1* was on the left, initial reaching trajectories on trial *n* were biased towards the left (independent of the target location in trial *n*). Similarly, Jax and Rosenbaum observed that depending on whether an obstacle was present versus absent on the previous trial, the curvature of the hand’s path was primed (hand path priming effect; Jax & Rosenbaum, 2007). In addition, Rosenbaum, Weber, Hazelett, and Hindorff (1986) found motor plans to be programmed by changing only those aspects of the last motor plan that are required for the current movement (parameter remapping). In a sequential pick-and-place task (several grasping movements with different target objects), Hesse and Deubel (2010) found the grip orientation of the last movement segment to influence the grip orientation of the preceding movement segments. Taken together, these results suggest that intertrial history influences grasping parameters in both the planning and the actual execution stage of the movement, which shows dorsal features from previous motor programs have the ability to influence spatial properties of the current motor program.

In summary, both spatial properties (Chapman, et al., 2010; Jax & Rosenbaum, 2007; Rosenbaum, et al., 1986) as well as non-spatial properties of recent action and experience (Hesse, et al., 2008) have been demonstrated to affect movement planning and execution on a given trial. Crucially, an influence of non-spatial properties of recent experience has hitherto not been examined in an intertrial paradigm - that is, in the previous intertrial studies, only one of the two factors object location or object presence was variable across trials, at a time. Therefore, in the present chapter, we wanted to investigate whether intertrial priming effects of object features are location specific or can be generalized over changes of location. That is, our main goal was to examine whether feature-based intertrial effects are present when the object in trial *n* is presented in a spatially different location compared to trial *n*-1. Specifically, can features of trial *n*-1 be transferred to a spatially new location in trial *n*? Hesse, et al. (2008) found feature-based priming effects in a preview study without changing the location of the object, while Jax and Rosenbaum (2007) found spatial properties to influence behavior from trial to trial by changing the location of the targets position from trial to trial without changing features of the target object. To dissociate between the feature-specific and the location-specific modulation of the two previous studies, we will combine both modulations in one experiment. Specifically, are intertrial effects for non-spatial features specific to the location where they arise from? Or are they stored in general memory traces, which modulate performance, even if the movement is programmed to a different location?

In more detail, in the present experiment, participants had to grasp either a wine or water glass and place it at a predetermined position. Only one glass (wine or water) was presented on a given trial and its (starting) position was varied to be either on the left or the right side with respect to the initial resting position of the grasping hand (always the right hand). This task and setup permitted us to address the following questions: Can features of trial *n*-1 be transferred to a spatially new location in trial *n*? That is, would the object of the previous trial be able to bias the current movement in terms of faster initiation reaction times (RTs) and movement times (MTs) for repetitions versus changes of movement parameters independent of the location of the target in trail *n-1*? What specific parameters (previous location of the target, previous feature (type of glass) of the target, or both) of the natural grasping movement are influenced by recent trial history with a relatively long intertrial interval? Does the left/right (starting) position of the object grasped on the previous trial bias the motor plan of the current movement into the direction on the previous trial? We expected intertrial effects in terms of RTs to reflect intertrial modulations on movement planning (including perceptual coding) stages and effects in terms of MTs to reflect intertrial modulations on movement execution stages.

Method

Participants. 20 undergraduate and graduate students (5 male; all right-handed; all with normal or corrected-to-normal vision; median age of 25 years) participated in a 40-minute experimental session for payment (8 euro per hour).

Apparatus and stimuli. Participants sat comfortably on an adjustable chair in a well-lit room, in front of a wooden board (72 x 50 cm), which served as presentation surface for the stimuli. Participants were wearing liquid-crystal (LC) shutter glasses (Milgram, 1987) and on their action hand (the right hand) motion tracking sensors. Two standard glasses (one water glass, 14.5 cm in height and 350 grams in weight, and one wine glass, 21 cm in height and 200 grams in weight) were used as the target objects. At the beginning of each trial, participants had to bring their right hand into the initial resting position, gripping a small knob 1 cm in height and 0.5 cm in diameter with their right-hand thumb and index finger located in the middle of the near end of the board, some 15 cm in front of the participant. Then, the LC shutter glasses went opaque, and the experimenter placed a glass at one of two possible starting positions, either that on the left or that on the right; both positions were marked with red foam rubber patches and situated about 18 cm further away from the participant than the resting position. Next, the shutter glasses opened and participants had to pick up the glass and place it at a fixed target position as fast as possible (see Figure 1). This position was located in the center of (the top surface of) a box, also marked with a piece of red foam rubber, which was 25 cm more distant from the participant than the nearer starting positions and measuring 30 cm x 20 cm x 15 cm (width × depth × height). The purpose of the foam rubber at the starting and end positions of the to-be-performed pick-and-place movement as well as on the experimenter's table was to reduce the noise of the glass when it was placed (by the experimenter) on the starting position or replaced with another glass.

The speed of the grasping movements was recorded using a Polhemus Liberty (Polhemus Inc., Colchester, VT) 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 in order to measure the transport component of the movement (wrist marker). Participants wore LC shutter glasses, to ensure suppression of vision during the time between the trials.

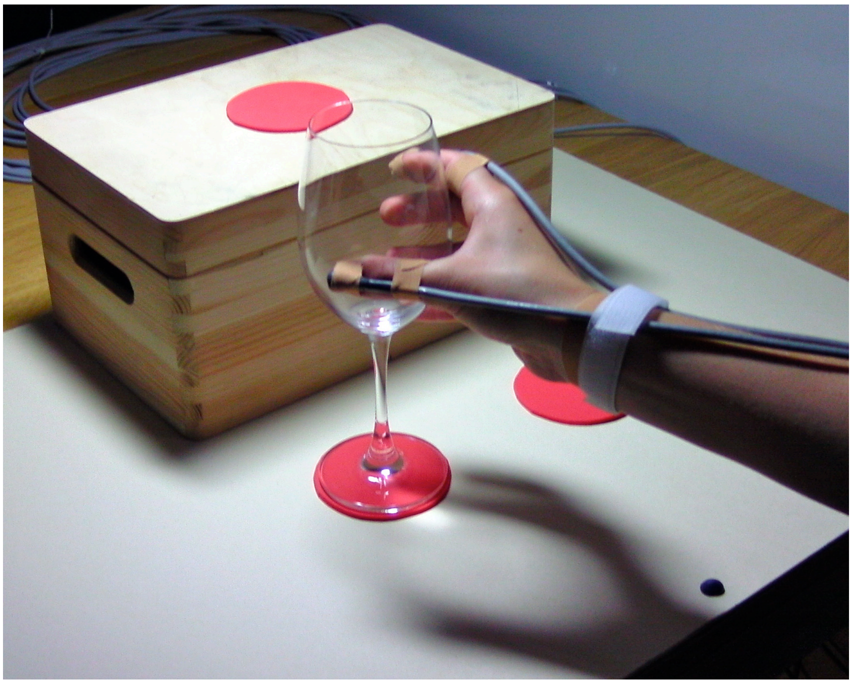

Figure 1. A picture of the experimental setup with a participant during the experiment. The resting position was marked with a small knob on the front end of the setup. The two red foam rubbers on the bottom were used as starting resp. pick positions for the target object and one red foam rubber on the box as the target resp. place position. The Polhemus tracker device was attached to the right thumb, index finger and the wrist.

Procedure. Participants started each trial with their right-hand index finger and thumb at the resting position on the tabletop gripping a small knob 1 cm in height and 0.5 cm in diameter (Figure 1). In the interval between trials, the LC shutter glasses were closed to eliminate vision. This permitted the experimenter to place the target object on the table without this being seen by the participant. After the experimenter had placed the target object on its new starting position, the experimenter initiated the trial manually by pressing a key on the experimenter's computer keyboard. This key press triggered the opening of the LC shutter glasses, which was accompanied by an auditory signal (a 1000-Hz beep of 100-ms duration) as an additional start signal.

Participants were instructed to plan and initiate the movement as soon as the shutter glasses opened. After planning the movement, participants moved to grasp the glass, lifted it up, and placed it at the end position on top of the target box. Thereafter, they moved their hand back to the resting position, leaving the glass on the box. After 2.5 seconds, participants heard another auditory signal, which indicated the end of the trial, and the LC shutter glasses closed. Subsequently, the experimenter returned the glass and prepared the next trial. Participants were told to move at a natural speed, rather than as fast as possible, so as to ensure natural grasping. Note that the participants were instructed to grasp the wine glass by the goblet, and not by the stem, which ensured that the type of grip and the grip aperture of the hand were about the same for the two (wine and water) glasses.

In all conditions, the participants were allowed 2.5 seconds to execute the pick-and-place movement. If this time limit was exceeded, the trial was classified as an error and repeated later on, at a random point, in the experiment. Each of the target objects (wine or water glass) was presented 25 times at each starting position (100 trials in total, not including the practice trials). At least four practice trials were given before the experiment started (each movement condition appeared at least once) to familiarize the participants with the task. All trials were presented in a randomized order during the experiment.

Data Analysis. Data were analyzed using R (R Development Core Team, 2009). The experimenter recorded an error when the pick-and-place movement was executed improperly (e.g., when the hand ‘crashed into’ the glass, when the box was hit when lifting the glass onto the box, or when the movement was too slow). In that case, the error trial and the following trial were removed from analysis (less than 1% of all trials). Additionally, a given trial *n* was excluded from analysis if there were missing (motion sensor) raw data on trial *n-1* (about 5% of all trials).

RT was defined as the interval between the opening of the LC shutter glasses (when the trial setup became visible) and movement onset. Movement onset was defined as the point in time at which both thumb and index finger exceeded a predefined velocity criterion of 0.01 cm/msec. MT was defined as the interval between movement onset and the grasping of the glass. The time of grasping the glass was quantified as the minimum velocity of the wrist when the thumb reached inside a predefined area in which the target object was situated. MT2, that is, the time taken to put the glass onto the box, was defined as the time from grasping the glass at the starting position to the placement of the glass at the target position on top of the box. MT2 was measured in the same way as MT, though with a different predefined target area (see Fig. 2 for an illustration of the complete pick-and-place trajectory and the velocity path for the wrist). Total time was calculated as the sum of RT, MT, and MT2.

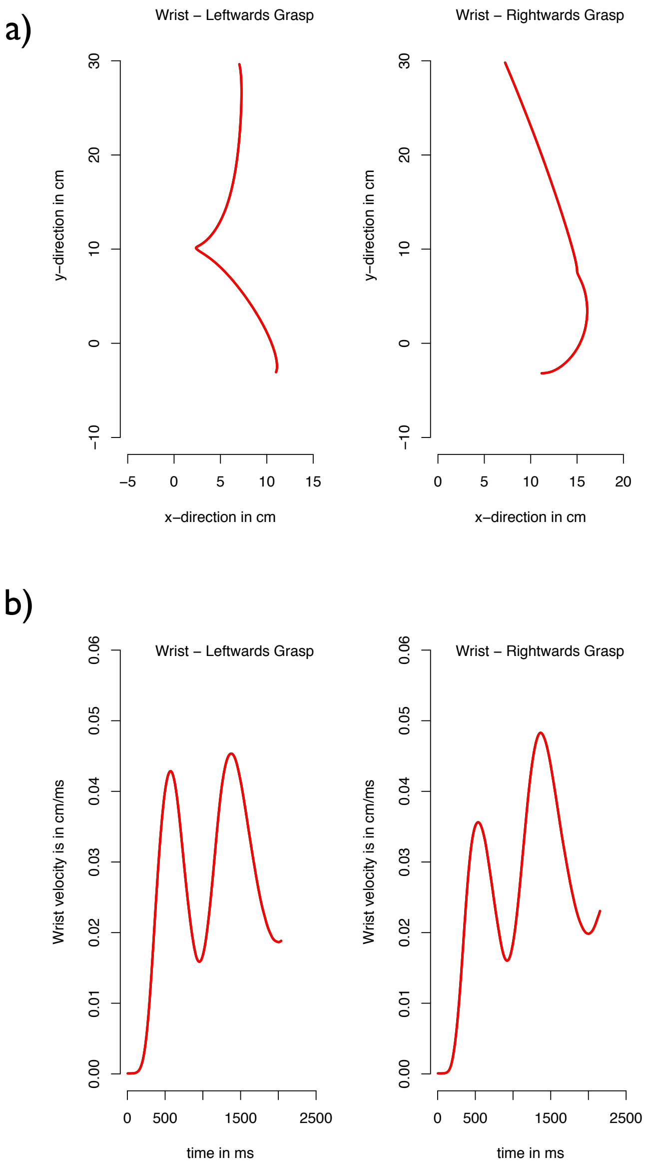

Figure 2. The pick-and-place wrist movement path (a) and the wrist velocity path (b). In a, the movement is shown in 2 dimensions (X, Y) as seen from above. In the left figure, the pick-and-place movement to the left target position is shown and in the right figure to the right target position. In b, wrist velocity was plotted in cm/ms. In the left figure for a leftwards grasp and in the right figure for a rightwards grasp.

For data analysis, repeated-measures analyses of variance (ANOVAs) were performed with the factors object transition (same object or different object on consecutive trials), position transition (same or different starting position on consecutive trials), location of the object (left- or right-side starting position) and target object (water or wine glass). Dependent variables analyzed were RT, MT, MT2, and total time. The ANOVA main effects (*F*- and *p*- values) of object transition, position transition, object location, and target object and the exact mean values with their associated standard error (in ms) are reported in Tables 1 and 2.

Results

RT. The ANOVA of the RTs revealed the main effects of object transition, object location, and target object to be significant (see *F*- and *p*- values in Table 2 and numerical values in Table 1). Of main interest for the current chapter, RTs were faster when grasping the same target object (whether a wine or a water glass) on two consecutive trials compared to grasping two different objects. Additionally, RTs were faster to objects located on the right side, as compared to the left side, of the starting position (i.e., to objects ipsilateral, rather than contralateral, to the hand with which the movement was made). And RTs were faster to water than to wine glasses. By contrast, whether or not the glass to be grasped was located at the same or different starting positions on consecutive trials had no effect on RTs. No interactions were significant (see Appendix for a listing of all interaction statistics).

Table 1. Values of dependent measures for object change, position change and location of object

Trial type	RT (ms)	MT (ms)	MT2 (ms)	Total time (ms)
Object				
same object	361 (14)	581 (14)	1193 (42)	2131 (53)
different object	370 (15)	587 (15)	1196 (39)	2154 (52)
Position				
same position	365 (15)	585 (14)	1193 (40)	2140 (52)
different position	365 (14)	584 (15)	1195 (41)	2145 (53)
Location of object				
Right	361 (14)	574 (15)	1212 (41)	2143 (53)
Left	370 (15)	595 (14)	1177 (39)	2141 (52)
Target object				
water glass	358 (14)	578 (14)	1169 (40)	2104 (53)
wine glass	365 (15)	581 (14)	1235 (41)	2181 (52)

All values shown as mean (standard error).

MT. The ANOVA of the MTs (i.e., the time between movement onset and the grasping of the glass) revealed the main effects of object transition and location of object to be significant (see *F*- and *p*-values in Table 2 and numerical values in Table 1). MTs became faster when grasping the same object on two consecutive trials, compared to grasping two different target objects. Additionally, MTs were faster for picking up an object positioned on the ipsilateral side (relative to the moving hand). MTs were not influenced by whether the object to be grasped was located on the same side versus on the different side on consecutive trials, and they were not influenced by whether it was a wine or a water glass. No interactions were significant (see Appendix for a listing of all interaction statistics).

MT2. The ANOVA of the MT2s (i.e., the time from grasping the glass at the starting position to placing it at the target position on top of the box) revealed only the main effects of object location and target object to be significant (see *F*- and *p*-values in Table 2 and numerical values in Table 1), whereas those of object and location transition were not. In this respect, the pattern of results for the MT2s is different from that for the MTs. The main effect of object location was due to the placing of the object being accomplished faster when the object's starting position was contralateral (left side), rather than ipsilateral (right side), to the (right) hand carrying out the movement. And water glasses were placed overall faster than wine glasses. Of the interactions, only that between target object x object location was significant [*F*(1,19)=5.22, *p* = .03]. This interaction was owing to the fact that the effect of the starting position location on placing the object (i.e., on the MT2s) was less marked for the water glass than for the wine glass (see Appendix for a listing of all other interaction statistics).

Total time. The ANOVA of the total times revealed the main effects of object transition and target object to be significant (see *F*- and *p*-value in Table 2 and numerical values in Table 1): the whole movement was faster when the type of glass was repeated on consecutive trials, compared to when it switched. Additionally, the pick-and-place task was accomplished overall faster with water glasses than with wine glasses. The main effects of object location and position transition were not significant. Of the interactions, only that between target object and object location was significant [*F* (1,19)=8.66, *p* = .008]. This interaction reflected the fact that the pick-and-place movement was executed faster when water glasses, as compared to wine glasses, were placed on the right side (see Appendix for a listing of all other interaction statistics).

Table 2. ANOVA results

Factor	F	p
	Reaction time	
object transition	7.94	.01
position transition	0.02	.88
object location	7.04	.02
target object	5.07	.04
	MT	
object transition	7.98	.01
position transition	0.00	.96
object location	4.75	.04
target object	0.43	.52
	MT2	
object transition	0.69	.42
position transition	0.69	.42
object location	12.15	.002
target object	21.14	.000
	Total time	
object transition	7.16	.01
position transition	0.42	.52
object location	0.02	.90
target object	21.25	.000

All with 19 degrees of freedom and exact p values.

Discussion of Chapter 4

Summary of findings. The present chapter was designed to examine whether feature-based intertrial effects are present when the object in trial *n* is presented in a spatially different location compared to trial *n*-1. RTs, MTs, and total times were modulated by intertrial object transition independent of the location in trial *n-1*. That is, repeating the same glass across two consecutive trials yielded faster initial movement planning and faster grasping movements compared to changing the type of glass. By contrast, MT2 (the time from grasping/picking to placing the object) was not affected by the object transition across trials. For position transition, no significant effects were observed in any of the four measures (RTs, MTs, MT2s, total times); that is, merely repeating (vs. changing) the object's starting position across two trials did not influence the initial movement planning and the grasping (and placing) movements in the present situation. Overall, though, a glass was grasped faster when it was positioned on the side ipsilateral, rather than contralateral, to the effector (the right hand), though this effect was not seen in the MT2s and total times. And the water glass was handled faster in all movement components (though with only a trend in MTs).

History effects. The present trial-to-trial history effects are in line with Rosenbaum, Cohen, Jax, Weiss, & Van Der Wel (2007), who state in general terms that movements and movement parameters are never formed or programmed de novo for consecutive movements or trials, but are programmed according to the last movement sequence and the differences of the next movement sequence compared to the last sequence. The parameter remapping and the hand path priming effect provide evidence that changing a feature of a motor plan - in the present case: the glass (wine or water glass) - will slow down the planning and grasping parts (but not the transport part, since this part of the movement does not require a change in the movement program from trial to trial) of the movement. Similarly Hesse and Deubel (2010) found the grip orientation of the last movement segment to influence the grip orientation of the preceding movement segment, which is compatible with the results of the present chapter by showing that movement parameters are kept in memory for two consecutive trials. Supporters of the real-time view (e.g. Cant, Westwood, Valyear, & Goodale, 2005; Goodale, Westwood, & Milner, 2004; Westwood & Goodale, 2011) claim that the movement parameters proper (e.g., egocentric position of the target object) are only computed by the dorsal system when actually performing a target-directed action. According to this notion, no history effects should be observed in any kind of grasping movements. We demonstrated however here that such intertrial effects can also be observed in natural tasks with intertrial intervals of at least 6.5 sec. The present results provide first evidence that intertrial motor priming effects of object features are location unspecific. In other words, non-spatial memory can modulate performance in ongoing trials, even if the movement is programmed to a different location.

For the transport component of the movement (i.e., the MT2s), no intertrial transition effect was observed. The grasping movement from the picking part of the movement to the placing part is the same across different conditions. In addition, changes of object or location should not require significant differences in the movement plan (Rosenbaum, et al., 2007).

Role of the intertrial interval. Intertrial history effects imply a memory trace of the last trial (Dorris, Paré, & Munoz, 2000). If this memory trace decays, the intertrial history effect should also diminish as a function of the interval between two consecutive trials. Indeed, evidence for such a decay of memory traces has been found by Jax and Rosenbaum (2009), who examined the influence of the interval between prime and target presentation on different movement parameters. The priming effect in Jax and Rosenbaum's study was reduced with higher prime-to-test intervals (250-, 600-, and 1000-ms). Given this, we performed an additional (relatively rough) analysis of the data obtained in the current chapter to examine for an effect of the length of the intertrial interval. In the current chapter, the intertrial object transition effects (in terms of movement initiation RTs) were smaller when the interval between two successive trials was longer, rather than shorter, than the median intertrial interval (of 8.2 secs). The effect of intertrial object transition (repeating vs. changing the type of glass on two consecutive trials) was 15 ms (a post-hoc comparison revealed the intertrial object transition effect statistically to be greater than zero, $t(16)=-2.60$, $p<.05$) for short intervals, but only 3 ms for long intervals (a post-hoc comparison revealed the intertrial object transition effect statistically not to be greater than zero, *t*(16)=-0.49, *p*=.63). A more fine-grained analysis of this intertrial interval effect could not be conducted due to the low number of trials after the data set was (median) split. Although the present data were analyzed only post-hoc for intertrial interval effects, the results show that the memory trace from the last trial is less strong with longer intertrial intervals and that this effect is also evident in natural grasping situations.

Intertrial position effects. Of note, no effects were found for (starting) position transition, which could have been expected from the literature (Chapman, et al., 2010; Dorris, et al., 2000). In particular, one would have expected shorter movement planning and MTs when repeating (vs. changing) the starting position on two consecutive trials; for instance, Chapman et al. (2010) found that the initial reach trajectories on a given trial *n* were shifted in the direction of the location of the target on the previous trial *n-1*; Dorris et al. (2000) found saccadic reaction times to be faster when repeating the same movement (saccade to a specific location), and Maljkovic and Nakayama (1996) found faster (manual) reaction times to targets at repeated target locations. One possible reason for the null-finding in the present chapter is that there exist different kinds of memory systems for spatial and non-spatial memories (e.g., Smith et al., 1995). There is, however, no evidence that one of these memory systems has a faster decay rate than the other as could be inferred from the results in the present chapter. In terms of the results in the present chapter one could argue that the decay for spatial memories is faster than the decay for non-spatial memories. Further research is needed to investigate the cognitive architecture of these two memory systems in more detail.

Positional effects. An additional finding was that the object in space ipsilateral to the effector (the right hand) was found to be handled faster in terms of both the RT and the MT component of the grasping movement. Prolonged times for movements across the midline to the opposite side of the effector hand have been found in the literature in two studies (see Fisk & Goodale, 1985, for an explanation of these effects; Hesse & Deubel, 2009). Fisk and Goodale (1985) argued that the neural systems responsible for the programming of grasping movements are hemispherically organized and that prolonged times for movements in contralateral space to the effector are only found when grasping across the body axis. Therefore, the motor program responsible for the movement has to cross to the opposite hemisphere with the result of slower movement initiation. Two possible reasons why no results were found for the placing part of the movement (MT2) in the present chapter could be that (i) the target position was exactly in the middle of the box and therefore neither ipsi- nor contralateral or that (ii) the movement parameters for MT2 had to be programmed only on the first trial of the experiment, since this part of the movement was the same on consecutive trials (Rosenbaum, et al., 2007).

Glass type effect. The water glasses required a shorter movement planning time (RT) and a shorter MT2 for the transport component of the movement. This finding can be expected as wine glasses are easier to break and therefore demand more fine-tuned motor skills than grasping a water glass (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). Moreover, the wine glass was grasped by the goblet and not by the stem, which is an unfamiliar way to grasp a wine glass. In the current chapter, the interaction object transition x target object was never significant – this means that the different glasses had no influence on the history effects found in the current chapter.

Taken together, the data in Chapter 4 provide strong evidence that feature-based intertrial effects are present when the object in trial *n* is presented in a spatially different location compared to trial *n*-1. That is, features of trial *n*-1 were transferred to a spatially new location in trial *n*, i.e., non-spatial features are stored in memory traces, which are not bound to a specific location. Here it has been demonstrated for the first time that such non-spatial feature-specific intertrial effects can also be observed in natural grasping tasks with intertrial intervals of at least 6.5 sec. Chapter 5 is aimed at investigating in what specific way visual input causes automatic visuomotor priming and is related to the current chapter in that it deals with the formation of motor programs. In other words, Chapter 4 focused on the influence of previous actions on the current action while Chapter 5 aims to investigate the influence of previous perception on the following action.

CHAPTER V

Visuomotor priming effects in grasping depend on the quality of cue processing

The idea that perception and action are coupled can be traced back until William James (James, 1980) and has been reintroduced into the current debate as the *common coding* theory (Prinz, 1984). The common coding theory links perception and action such that perceived events automatically activate the corresponding brain networks for that specific action. That perceptual events influence motor behavior has been shown empirically in various paradigms with different behavioral and physiological methods and has been referred to as visuomotor priming (e.g., Craighero, Fadiga, Umilta, & Rizzolatti, 1996), affordances (e.g., Cisek, 2007), automatic imitation (see Heyes, 2011 for a review) and has been tagged as the mirror neuron system (e.g., Craighero, Metta, Sandini, & Fadiga, 2007). The term and concept of *affordance* was first introduced by James Gibson (Gibson, 1977) and described as *action possibilities.* Objects have, in his view, an automatic ability to afford an action. *Automatic imitation* (Heyes, 2011) extends the concept of *visuomotor priming* (Craighero, et al., 1996) in that not only objects, but also actions of other human beings lead to automatic activation of the corresponding motor programs.

Although there is growing evidence for the strong linkage between action and perception, some aspects are still controversially discussed (Amazeen & DaSilva, 2005; Cant, Westwood, Valyear, & Goodale, 2005) and not fully understood (Garofeanu, Króliczak, Goodale, & Humphrey, 2004). Especially, there is a debate about the robustness of visuomotor priming effects, which are reported in some studies (Craighero, Fadiga, Rizzolatti, & Umilta, 1998; Craighero, et al., 1996; Kiefer, Sim, Helbig, & Graf, 2011; Olivier, 2006) and were not found in others (e.g., Cant, et al., 2005). The current chapter investigates what factors are responsible for visuomotor priming effects to be observed. The debate about the coupling of the perception and action system is explained by means of the visuomotor priming paradigm with both behavioral as well as physiological findings arguing for and against the linkage of perception and action.

Perception-action coupling – evidence for visuomotor priming. Merely perceiving an object or an action has been shown to facilitate the corresponding action (Craighero, et al., 1996). For instance in a grasping task, with a semantic cue displaying the upcoming orientation of the target bar and an additional cue (a picture of the to be grasped bar) was shown on the computer screen right before the grasping movement started (Craighero, et al., 1996). This additional cue could be congruent with the target object (same orientation), incongruent (different orientation), or neutral (with just a circle). The results showed that the motor system can be influenced by previously seen cues, even when the movement is already programmed by the semantic cue. The automatic coupling between perceiving objects and acting upon them has been replicated in numerous behavioral studies showing visuomotor priming effects (Craighero, et al., 1996; Hesse, de Grave, Franz, Brenner, & Smeets, 2008; Vingerhoets, Vandamme, & Vercammen, 2009). Additionally, watching short video sequences showing a grasping movement facilitates object recognition (Helbig, Steinwender, Graf, & Kiefer, 2010).

In agreement with classical studies on visuomotor priming (e.g., Craighero, et al., 1996) and a the common coding theory (Prinz, 1984), there is neurophysiological evidence for the strong link between perception and action. For instance, perception of objects automatically activates appropriate motor representations (Grèzes & Decety, 2002). Areas known to be involved in motor representations (areas within the inferior parietal lobe, in the premotor cortex, in the SMA-proper and in the inferior frontal gyrus) were active among different tasks (Grèzes & Decety, 2002). Grèzes and Decety showed that objects have the ability to automatically activate specific motor representations, with a question still remaining unsolved, why grasping movements to incongruent objects take longer than to congruent objects. The earlier described RT differences between congruent and incongruent trials seem to arise in the brain by producing a competition between the seen cue and the action of the given trail (Grèzes, Tucker, Armony, Ellis, & Passingham, 2003). If in one trial the cue object and the target object are different (incongruent trial), the competition within the involved brain network is greater and the time to grasp the object takes longer, because this competition has to be resolved first. Knowing the brain mechanisms involved in visuomotor priming, the question of the time course of visuomotor priming still remains open. Visuomotor priming affects already early visual areas with fast ERP effects found around 150 ms after target onset when the cue was shown as a picture, while it also has been shown to affect later components (Kiefer, et al., 2011). The late N400 ERP component has been found when the cue was presented in a semantic way (Kiefer, et al., 2011) and thus showing that visuomotor priming effects can be elicited by both fast and slow pathways depending on the cue presented. There are numerous behavioral and psychophysical examples for the coupling between the perceptual and the action system by showing visuomotor priming and automatic imitation effects, but some researchers still challenge these effects by claiming the independence of the perception and action system.

Perception-action dissociation – evidence against visuomotor priming. Evidence for a distinction between the perception and action system has a long scientific history as well with neurophysiological, psychophysical and patient studies. Two distinct streams for processing perceptual information have first been proposed using primates with lesions (Ungerleider & Mishkin, 1982). The ventral stream is responsible for the perception of objects whereas the dorsal stream is responsible for the control of action resp. perception of action. First evidence from human beings came from neuropsychological patients with brain damage of either the occipitotemporal cortex resp. the posterior parietal cortex (Goodale & Milner, 1992; Milner & Goodale, 2008). Following damage to the occipitotemporal cortex, patients could not identify the presented objects, but were able to grasp them in the right way. While patients with damage in the posterior parietal cortex could correctly perceive the presented object, but were unable to program an appropriate grasping movement. Similar results for a dissociation between perception and action have been found in a visuomotor priming task (Cant, et al., 2005), in grasping tasks using perceptual illusions (Amazeen & DaSilva, 2005) and visual search tasks (Brown, Moore, & Rosenbaum, 2002). Cant et al. showed visuomotor priming effects to appear only in memory-guided grasping movements, but not in visually-guided grasping movements. In the memory-guided grasping conditions, the grasping movement had to be planned from memory without having a direct visual input of the target object, while in the visually-guided grasping condition, the target object was visible throughout the whole grasping movement. The findings by Cant et al. are in stark contrast to the findings by Craighero et al. (1996), using the same setup and stimuli in their experiments. The only difference was in the memory-guided grasping conditions with an interval of only 100 ms (Craighero, et al., 1996) between priming stimulus and the onset of the response and 1250-1750 ms in the study by Cant et al. (2005). It seems that the contribution of the perception and action system to reaching and grasping movements are distinct from each other.

Specific motivation of the present chapter. The current empirical basis for visuomotor priming seems incompatible with both the perception-action coupling account (e.g., Prinz, 1984) and the perception-action dissociation account (e.g., Milner & Goodale, 2006). Classically, visuomotor priming is thought to affect actions by the simple presence of visual objects or stimuli (Craighero, et al., 1996; Grèzes, et al., 2003; Helbig, et al., 2010), while later, visuomotor priming was modified in such a way that the graspable cue object has to be attended (Craighero, Fadiga, Rizzolatti, & Umiltà, 1999). Are there still visuomotor priming effects when attentional resources are being guided to a spatially different location than the cue? This question was investigated in an automatic imitation task using two overlapping stimuli with directing the participants' attention to one of the two stimuli, which could either be a grasping hand or a rectangle that varied in its color (Chong, Cunnington, Williams, & Mattingley, 2009). Interestingly, when attending to the rectangle (spatially overlapping with the grasping hand), the automatic imitation effect was no longer visible. In a further experiment by Chong et al., the question was investigated whether automatic imitation effects depend on the allocation of attention to the cue relevant location of the grasping hand. Attending to a specific feature of the grasping hand (such as laterality of the presented grasping hand) does not cause an automatic imitation effect, but only when attention was allocated to the relevant spatial location of the grasping hand. In the present chapter on visuomotor priming, we investigated the issue of task-relevance by introducing a simple memory task, where participants are asked to remember the identity of the cue that is not relevant to carry out the task successfully, but relevant for the complete encoding of the cue object identity. It seems that specific features of objects are processed according to the current task instructions (Sereno & Amador, 2006). Sereno and Amador recorded the activity from the lateral intraparietal area (LIP) in the monkey and found a significant amount of neurons firing according to task instructions (object vs. location specific). A difference between the automatic imitation study (with a 2D grasping hand cue) by Chong et al. (2009) and the present chapter is that the visuomotor priming paradigm was used in the present chapter with the cue and target being natural objects. To test if the results by Chong et al. (2009) can be generalized to other paradigms, we investigated whether feature-specific attention to the cue object is necessary in the visuomotor priming paradigm to facilitate the grasping movement in the congruent condition.

Can the visuomotor priming effect be manipulated by the duration the cue object is presented before the action onset? It appears that an *active representation* of the cue object is able to cause the visuomotor priming effect, independent of the visibility of the target object during the grasping movement (Tucker & Ellis, 2004). Therefore viewing the cue object at the onset of the grasping movement or already before in a preview condition of the cue object, should both generate the visuomotor priming effect. One difference between the studies finding visuomotor priming effects (Craighero, et al., 1999; Craighero, et al., 1996) and a study finding no visuomotor priming effects (Cant, et al., 2005) was that the priming interval between the cue presentation and the action was much longer (100 ms vs. 1250-1750 ms). During that time the stored memory trace of the cue might have been decayed. We will approach this issue in the present chapter by manipulating the viewing time of the cue, which could be either the simultaneous onset of the trial with the cue and target object or by inserting a preview condition of the cue before the start of the trial.

Aim of the present chapter. The general question to be investigated in the present chapter is, whether attention to the cue object (Craighero, et al., 1999) and a long enough presentation time of the cue object (Tucker & Ellis, 2004) are enough to generate the visuomotor priming effect? The other possibility of generating visuomotor priming effects is that the feature of the cue, which can be congruent or incongruent, has to be task relevant as well (Chong, et al., 2009). The aim of the present chapter was to investigate these two potentially important factors guiding visuomotor priming: (i) cue exposure time and (ii) the quality of cue processing. If visuomotor priming is not dependent on the duration the cue object is visible, than viewing the cue object longer should not influence visuomotor priming. The quality of cue processing, the second potential factor guiding visuomotor priming, is the way reflecting the way the cue is processed. Quality of cue processing is defined in the present chapter as the way the cue is perceived and processed: in one experimental condition, we ensure that the identity of the cue object is fully processed and remembered, whereas in the other experimental condition, participants saw the cue object (the only object in the visual scene) without further instructions. We investigate that the better the quality of cue processing, the stronger is the effect of visuomotor priming (Chong, et al., 2009). We used a pick-and place task with natural objects (wine or water glass), using identical objects as cue and target objects. Two experimental conditions for cue exposure time (simultaneous vs. delayed cue-target presentation) were combined with two kinds of cue processing quality (cue memory task vs. no memory task) in a visuomotor priming paradigm (see Table 1). The cue exposure time was manipulated by either showing the cue and the target object at the same time (simultaneous cue-target presentation) or by showing the cue before the target object in a preview condition for 1 sec (delayed cue-target presentation). The idea of the cue exposure time was that the participants in the delayed cue-target presentation had enough time to look at the upcoming cue and process all relevant features of the cue before the onset of the movement. In the simultaneous cue-target presentation condition, participants had to carry out the movement without prior knowledge of the cue. The quality of cue processing/feature relevance was manipulated in one condition in which participants were instructed to remember and reproduce the identity of the cue object of a few random trials in the experiment (memory task). In another separate experiment, the pick-and-place movement was carried out without any additional task (no memory task). The quality of cue processing manipulation ensured that the identity of the cue object was fully processed (memory task) and remembered until the movement was carried out.

In most visuomotor priming studies, only the RT (the time from the presentation of the target object until the initiation of the movement) was measured (Cant, et al., 2005; Craighero, et al., 1996; Helbig, et al., 2010), while in the present chapter, we additionally measured the movement time (MT1; the time from the onset of the movement until the target object is touched) and the transport component (MT2; the time from picking up the target until placing it onto the box). It seems possible, although never measured, that visuomotor priming effects do not only influence the movement planning stages (that includes the initiation time), but also the movement execution stage (both the MT1 and the MT2).

Table 1. Illustration of the four different experiments and the respective conditions.

	no memory task	**memory task**
simultaneous cue-target presentation	Experiment 1	Experiment 2
delayed cue-target presentation	Experiment 3	Experiment 4

Methods

Participants. All participants were right-handed university students with normal or corrected-to-normal vision who were either paid or received course credit for their participation. The experimental session lasted approximately one hour including the instruction and the setup of the participant. All participants gave written informed consent. Twenty-two participants took part in Experiment 1 (7 male, median age 26). Seventeen were included in the analysis as 5 had to be excluded due to damaged data or due to very few (< 30) valid trials. Sixteen volunteers took part in Experiment 2 (3 male, median age 26). Four participants had to be excluded due to damaged data or very few (< 30) valid trials. Twenty volunteers participated in Experiment 3 (7 male, median age 23). Two participants had to be excluded due to damaged data or very few (< 30) valid trials. Finally, nineteen volunteers (2 male, median age 25) participated in Experiment 4. Four participants had to be excluded due to damaged data or very few (< 30) valid trials.

Apparatus and Stimuli. Experimental setup was the same in all four experiments. Participants sat in a well-lit experimental cabin in front of a wooden table. A wine and a beer glass of approximately same weight (wine glass: 203g, beer glass: 229g), height (wine glass: 22.2 cm, beer glass: 18.1 cm) and circumference (wine glass: 8.1 cm, beer glass: 8.0 cm) served as cue and target objects. On each trial, the target object was presented on one central starting location and had to be placed on one out of two possible target locations onto a box. The relevant target location was indicated by a cue positioned directly behind the target location. All locations were marked with red rubber foam patches (see Figure 1 for an overview of the locations).

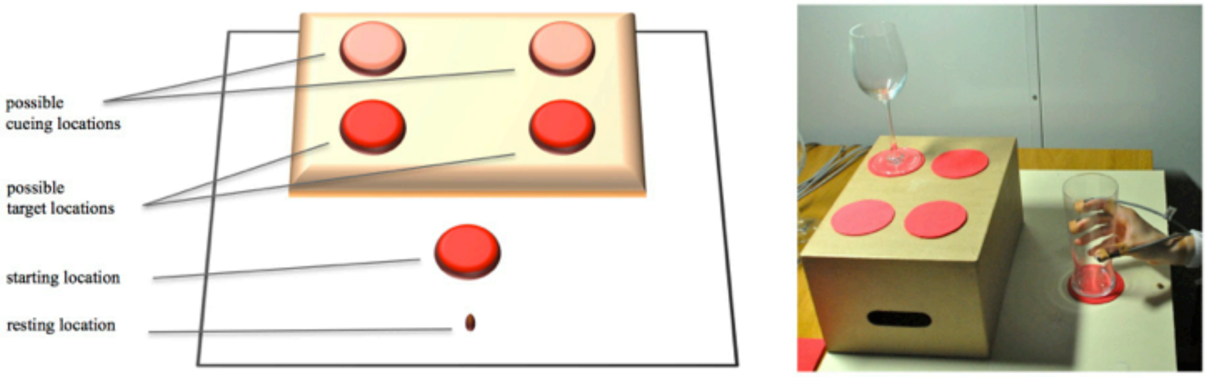

Figure 1. Left panel: schematic illustration of the possible cueing, target, starting and resting locations in the experimental setup. Right panel: the experimental setup.

Between the trials, participants left their right hand in a resting position marked by a central wooden pin in front of the starting location to which they had to hold on to with their thumb and index finger. Speed and trajectories of the grasping movements were recorded using a Polhemus Liberty electromagnetic motion tracking system with a sampling rate of 240 Hz. Four sensors were attached to the nails of thumb, index, middle finger and to the wrist of the right hand (using adhesive pastels and medical tape). Participants wore liquid-crystal shutter glasses (Milgram, 1987) to suppress vision between trials and allow the experimenter to rebuild the experimental setting. Participants received written and oral instructions and were allowed at least 8 practice trials, which were not included in the analysis.

Procedure. In all four experiments, the task was to pick up a target glass [wine glass ("wine-target") or a beer glass ("beer-target")] from the starting location and put it on one out of two possible target locations onto the box. For each trial the relevant target location was cued using congruent or incongruent objects (cue glass - "wine-cue" vs. "beer-cue"). The cue was the identical object in the congruent condition, i.e., the same beer glass ("beer-cue") when grasping a beer glass ("beer-target") was required for that trial, and the other object in the incongruent condition, i.e., the wine glass ("wine-cue") when grasping a beer glass ("beer-target") was required. The cue glass was positioned directly behind the target location (see Figure 1: cueing locations) and stayed there for the complete duration of a trial. Participants were instructed to move in natural speed and to grasp the wine glass by the goblet and not by the stem. Trials were initiated manually via key press by the experimenter as soon as all glasses had been placed in the correct positions. A trial then started with the opening of the shutter glasses, accompanied by a simultaneous auditory signal (a 1000-Hz beep of 100-ms duration).

In Experiment 1 and 2, participants were then presented with the cue glass in one of the cueing locations and the target glass in the starting location simultaneously. Participants had to grasp and lift up the target glass from the starting position as soon as the shutter glasses opened, to place it on the target location marked by the cue, leave the glass in the target location and return with their hand to the resting position. Another auditory (a 1000-

Hz beep of 100-ms duration) signal and the closing of the shutter glasses indicated the end of each trial after 2.5 sec, which was the maximum time participants were allowed for the completion of the movement. Each of the four possible glass constellations [cue glass (2) x target glass (2)] was presented 40 times, resulting in a total number of 160 experimental trials (not including practice trials).

In Experiment 3 and 4, the cue was already presented shortly before the target and the initiation of the movement: Trials started with the opening of the shutter glasses and the accompanying auditory signal and participants were presented with only the cue object in the relevant location for 1 sec. Then the shutter glasses closed again (for approx. 2 sec.) and re-opened with the target object at the starting location. As in Experiment 1 and 2, participants then had to pick up the target object and place it on the correct target location. Participants were again allowed 2.5 sec for movement execution. Each glass constellation was presented 30 times, yielding a total number of 120 experimental trials (practice trials not included).

In all four experiments, glass constellation and target location were randomized across trials. In Experiment 2 and 4, on every 20th trial on average, participants had to perform an additional memory task, namely to verbally report the identity of the cue glass (whether beer or wine) directly after the trial. Participants were informed about this additional memory task in the instruction and were told that on some trials the identity of the cue glass will be asked after completion of the trial.

Data analysis. Data analysis was conducted with R (RDevelopmentCoreTeam, 2006). Reaction time (RT) was defined as the time from the opening of the shutter glasses and the auditory signal until movement onset, which was when thumb and index finger exceeded a predefined velocity criterion of 0.01cm/msec. Movement time was divided into "grasping" and "placing time". The grasping time (MT1) was defined as the time from movement onset until grasping the glass. The placing time (MT2), i.e. the time to put the glass onto the box, was defined as the interval between grasping the glass and placing it on the target location. An error was defined when the movement was not executed properly: the maximum time of 2.5 sec allowed for movement execution was exceeded or when MT1 was < 200 ms and/or MT2 was < 500 ms. For each experiment, repeated measures ANOVAs were performed with the factors congruency (congruent vs. incongruent), target glass (wine-target vs. beer-target), cue glass (wine-cue vs. beer-cue) and target location (right vs. left) for RTs, MT1s and MT2s separately. All participants completed the memory task successfully with 100% correct answers in Experiment 2 and 4. Trajectories, i.e. the movement path, as well as velocity profiles of wrist, index finger and thumb were analyzed to illustrate the pick-and-place movement (see Figure 2).

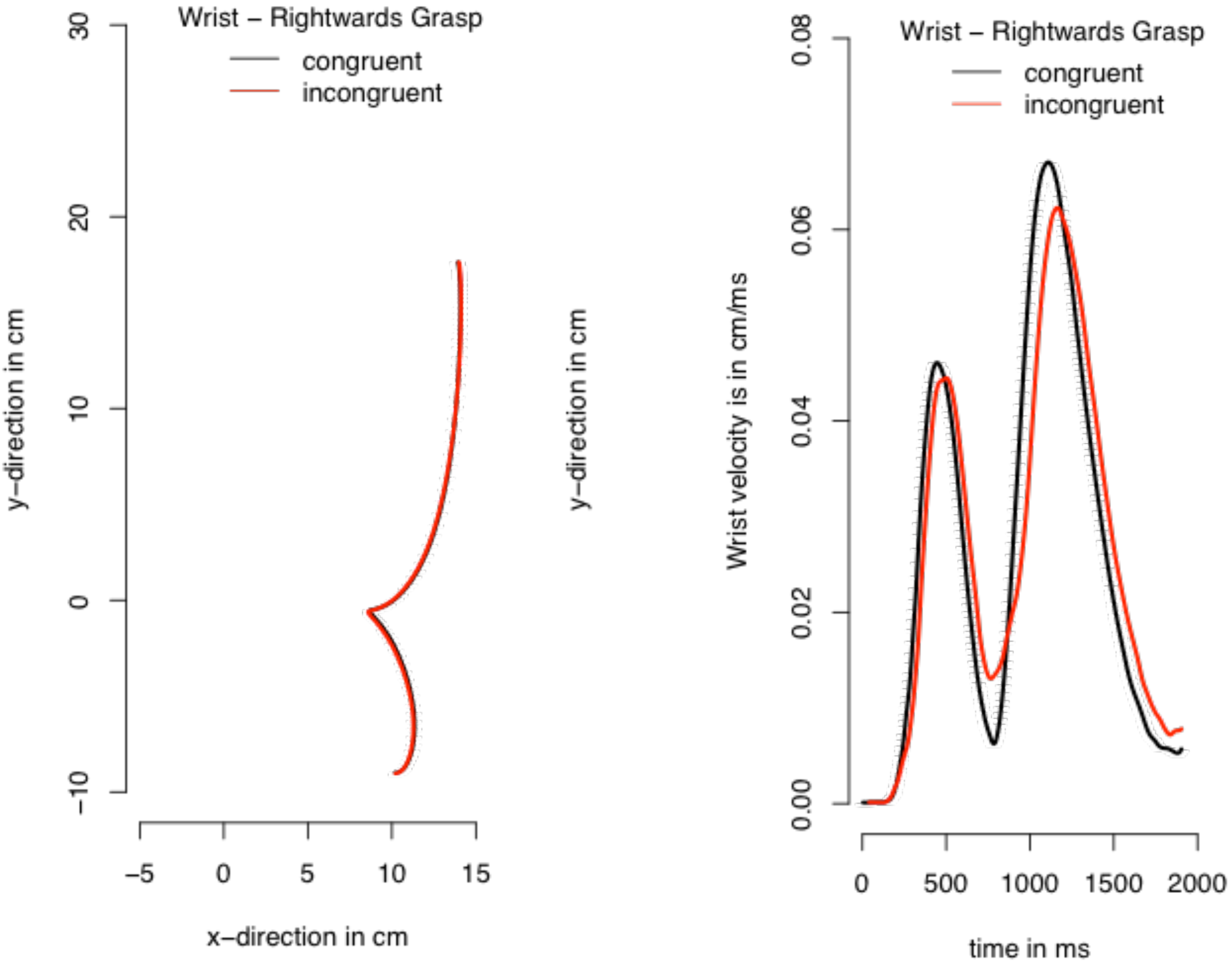

Figure 2. Left panel: movement trajectory of the wrist as seen from above for congruent vs. incongruent trials, plotted for a rightwards grasp. Right panel: Profile of wrist velocity in cm/ms for congruent vs. incongruent trials, plotted for a rightwards grasp.

Results

The ANOVA main effects (*F*- and *p*- values) and the exact mean values with their associated standard errors (in ms) can be obtained from Tables 2 and 3, respectively.

Experiment 1: simultaneous cue-target presentation & no memory task

RT. The ANOVA of the RTs, i.e. latency of movement onset, revealed no significant effect of any factor.

MT 1. The ANOVA of MT1, i.e. the time participants needed to grasp the target glass, revealed that beer glasses were grasped significantly faster than wine glasses, $F(1,16) = 31.53$, $p <.001$. There was no effect of congruency on participants' grasping time.

MT 2. The ANOVA of MT2, i.e. the time participants needed to place the glass on the target location, revealed that beer glasses were also placed significantly faster than wine glasses, $F(1,16) = 46.16$, $p <.001$. Again, there was no significant effect of congruency on the placing time.

Experiment 2: simultaneous cue-target presentation & memory task

RT. As for Experiment 1, there was no significant effect of any factor on RTs.

MT 1. For MT1, the ANOVA revealed a significant main effect of congruency; participants grasped the target glass significantly faster when the cue was congruent compared to when it was incongruent, $F(1,11) = 5.26$, $p =.042$.

MT 2. As for Experiment 1, beer glasses were placed significantly faster than wine glasses, $F(1,11) = 23.09$, $p <.001$. There was no significant effect of congruency on the placing time.

Experiment 3: cue-preview & no memory task

RT. The ANOVA of RTs revealed no significant effect of any factor.

MT 1. Only the factor target glass had a significant effect on MT1 in Experiment, $F(1,17) = 33.24$, $p <.001$. As in Experiment 1, grasping movements were faster when a beer glass had to be grasped compared to when a wine glass had to be grasped. There was no significant effect of congruency.

Table 2. ANOVA main effects for RTs, MT1 and MT2 for all four experiments

	Experiment 1			Experiment 3			Experiment 4			Experiment 2		
	(sim-nomem)			(sim-mem)			(del-nomem)			(del-mem)		
	F(1,16)			F(1, 11)			F(1, 17)			F(1, 14)		
	RTs	MT1	MT2	RTs	MT1	MT2	RTs	MT1	MT2	RTs	MT1	MT2
congruency												
F	0.64	0.31	1.15	1.07	5.26	0.00	0.07	0.22	1.12	0.07	4.64	0.79
p	.436	.585	.299	.323	.043*	.994	.788	.646	.304	.796	.049*	.390
target glass												
F	1.25	31.53	46.16	0.15	2.59	23.09	0.54	33.24	32.13	0.12	161.35	11.71
p	.279	<.001***	<.001***	.709	.136	<.001***	.472	<.001***	<.001***	.733	<.001***	.004**
cue glass												
F	1.17	0.16	0.01	1.32	2.56	0.03	0.05	0.01	0.29	0.37	1.11	10.39
p	.295	.692	.936	.276	.138	.872	.826	.911	.599	.551	.310	.006**
target location												
F												
p	0.70	2.49	0.09	1.66	0.04	4.38	1.38	0.02	11.73	8.73	0.01	0.81
	.415	.134	.768	.224	.850	.060	.257	.903	.003**	.010*	.923	.384

MT 2. The ANOVA revealed the main effect of location and of target glass to be significant, *F*(1,17) = 11.73, *p* =.003 and *F*(1,17) = 32.12, *p* <.001 respectively. Movements were faster when the target glass had to be placed on the right-side target location compared to left-side target location. Further, movements were faster when the target glass was a beer compared to when it was a wine glass. Congruency did not have a significant effect on MT2.

Experiment 4: cue-preview & memory task

RT. The ANOVA of RTs revealed a significant main effect of target location, *F*(1,14) = 8.73, *p* = .010: participants initiated their movements faster for the left target location, compared to the right target location.

MT 1. As in Experiment 2, the ANOVA of MT1 revealed the effect of congruency to be significant, *F*(1,14) = 4.64, *p* =.049: grasping movements were faster for congruent compared to incongruent trials . In addition, the interaction congruency x location turned out to be significant, *F*(1,14) = 18.15, *p* <.001; the slowing down in the incongruent condition mainly seemed to arise from trials in which the glass had to be placed on the left target location. Further, the effect of target glass was significant again, *F*(1,14) = 161.35, *p* <.001, resulting in faster grasping movements for beer glasses than for wine glasses.

MT 2. The ANOVA of MT2 revealed the main effects of the factors cue glass and target glass to be significant, *F*(1,14) = 10.39, *p* =.006 resp. *F*(1,14) = 11.71, *p* =.004. Placing of the glass was faster, when the target glass was a beer glass and also when the cue glass was a beer glass.

Table 3. Mean RT, MT1 and MT2 values and related standard errors (in brackets) for congruency, cue glass, target glass and target location in four experiments. All values in milliseconds.

	Experiment 1 (sim-nomem)			Experiment 3 (sim-mem)			Experiment 4 (del-nomem)			Experiment 2 (del-mem)		
	RTs	MT1	MT2	RTs	MT1	MT2	RTs	MT1	MT2	RTs	MT1	MT2
congruency												
congruent	354 (9)	493 (9)	1158 (21)	350 (12)	517 (8)	1099 (22)	336 (6)	525 (9)	1185 (16)	362 (9)	501 (8)	1035 (1
incongruent	357 (10)	493 (9)	1164 (20)	344 (12)	530 (9)	1099 (23)	335 (6)	524 (9)	1192 (16)	364 (10)	505 (9)	1029 (1
target glass												
beer	358 (10)	477 (9)	1117 (20)	348 (12)	512 (7)	1050 (24)	336 (7)	504 (9)	1157 (15)	365 (10)	482 (8)	1005 (2
wine	353 (9)	509 (8)	1205 (19)	347 (12)	535 (10)	1148 (19)	334 (6)	545 (8)	1219 (16)	361 (9)	535 (8)	1059 (1
cue glass												
beer	357 (9)	493 (9)	1161 (21)	350 (12)	520 (9)	1099 (23)	335 (6)	524 (9)	1187 (17)	364 (10)	505 (9)	1026 (1
wine	354 (10)	493 (8)	1161 (20)	344 (11)	527 (9)	1100 (22)	336 (6)	524 (9)	1190 (16)	362 (9)	502 (8)	1038 (1
target location												
left												
right	356 (9)	495 (9)	1162 (21)	350 (12)	524 (9)	1114 (24)	328 (6)	524 (9)	1208 (16)	359 (9)	503 (8)	1035 (1
	354 (9)	490 (9)	1169 (20)	344 (12)	523 (8)	1085 (21)	343 (6)	524 (9)	1169 (16)	367 (10)	503 (8)	1029 (1

Discussion of Chapter 5

Summary of findings. The present chapter was designed to examine two potentially important factors investigated in earlier studies (Chong, et al., 2009; Tucker & Ellis, 2004) influencing visuomotor priming, cue exposure time and quality of cue processing. Interestingly, only when introducing a simple memory task (as in Experiment 2 and 4), where it was necessary to remember the identity of the cue object, the visuomotor priming effect was found (in MT1) both in the simultaneous cue-target presentation and the preview-cue condition. In contrast, no visuomotor priming effects were visible when the task was carried out under classical visuomotor priming conditions (Cant, et al., 2005; Craighero, et al., 1996), with no memory task both in the simultaneous cue-target presentation and in the preview-cue condition. Additional results revealed that the pick-and place movement was faster, when the target object was a beer glass (all MT1s and MT2s, except MT1 in Experiment 2 were faster). Moreover, a novel visuomotor priming setup was used with a pick-and-place task using the same objects (beer and wine glasses) as cue and target objects, instead of presenting cue object on a computer display.

Specificity of visuomotor priming effects. From the data of the present chapter, we conclude that for visuomotor priming to occur, it is necessary to process the feature of the cue object that is relevant (congruent resp. incongruent) for visuomotor priming to occur, as opposed to simply attending the cue object. As in the present experiments, the cue object was cueing the location of the target object and therefore only the location of the cue was task-relevant, while it was not necessary to process the identity of the cue to fulfill the task successfully. Processing only the location of the cue object was not enough to generate the visuomotor priming effect. Previous studies on visuomotor priming used only simple cues and target objects (e.g. a left or right tilted bar), where the cue object could only change in one dimension (e.g. orientation), which was always task-relevant (e.g., Cant, et al., 2005; Craighero, et al., 1999; Craighero, et al., 1996). Therefore, the mere presentation of a visual stimulus was able to afford the motor representation necessary to induce the visuomotor priming effect, but it is not an *automatic* visuomotor priming effect in general, which was previously thought of (Craighero, et al., 1996; Grèzes, et al., 2003). The visuomotor priming effect was automatic, because the task and setup consisted of only one item on one location. In the present chapter, specific features of objects are processed according to the current task (Sereno & Amador, 2006), with location being relevant in all experiments, and the identity of the cue object being additionally relevant in only two of the experiments with the visuomotor priming effects. Thus, it could be that all aspects (location and identity) of the cue in the present chapter were processed to some extend and that the task-relevant aspects were enhanced or amplified and therefore generating visuomotor priming effects in the memory task. Independent of whether the cue's identity in the no-memory conditions was not processed at all or to only a weak degree – in order to produce priming effects, it needed to be task relevant and therefore processed more deeply.

The basic idea behind visuomotor priming is similar to the idea of automatic imitation that the object resp. action observed potentiates the appropriate action. Automatic imitation seems to occur only when attending to the feature that was relevant for the executed task (Chong, et al., 2009). Selective attention was playing an important role to distinguish the diamond-shaped outline from the grasping hand. The distinction between the outline and the grasping hand can be compared to the figure-ground segmentation (Baylis & Driver, 1995), where the ground is regulated away and only the figure is perceived. To solve the task in the study by Chong et al., participants' full attention was drawn to the diamond-shaped outline within the grasping hand (Chong, et al., 2009). In contrast, the present chapter was different, as participants were only viewing the cue-object and no other objects were present in the setup. Automatic imitation was also not seen when only the laterality of the grasping hand (decision whether the grasping hand was a right or left hand) was considered in the task (Chong, et al., 2009). In the present chapter, similar results were found, as visuomotor priming was only generated when the feature that could be congruent resp. incongruent was task relevant. Additionally, we can extend the findings by Chong et al. by using a different paradigm (visuomotor priming vs. automatic imitation) and a more natural setup with real cue and target objects.

It seems important to note that in previous visuomotor priming studies, the priming effect was only found in the initiation time (e.g., Chong, et al., 2009; Craighero, et al., 1996; Makris, Hadar, & Yarrow, 2011; Tucker & Ellis, 2001), while in the present chapter, visuomotor priming was visible in the pick time (MT1). There have been a few studies on visuomotor priming/automatic imitation measuring movement times as well (Chong, et al., 2009; Hesse, et al., 2008), but all of them found visuomotor priming effects only in the initiation time and not the movement time. One can hypothesize that the competition between competing motor plans is taking place during the movement as well by using online visual information. The competition between several motor plans has been described by the affordance competition hypothesis by additionally using online visual feedback to bias the executed movement until fully carried out (Cisek, 2007). Since in the present experiment, the target location was cued with a 100% validity, participants were able to program the final spatial location in advance. Thus, it could be that the competition between the cue object and the target objet was only resolved after the initiation of the movement (i.e., during the movement). In summary, the present chapter provides evidence that visuomotor priming does not occur automatically as suggested by many other studies (Craighero, et al., 1996; Grèzes, et al., 2003; Helbig, et al., 2010; Tucker & Ellis, 2004), but the specific feature of the cue object that can be congruent or incongruent, has to be task-relevant as well. Additionally, visuomotor priming affected only the movement time of the grasping movement, as opposed to previous studies detecting visuomotor priming in the initiation time of the movement.

No visuomotor priming effect when previewing the target. Having more time to view the cue object before the actual pick-and-place task does not generate visuomotor priming. Contrary to our findings, object affordance compatibility effects seem to arise, when the cue object is presented very briefly and then was masked (Tucker & Ellis, 2004). The basic idea behind the object affordance compatibility is similar to visuomotor priming, but using a categorization task. Common objects (such as a hammer, a pencil, an apple etc.) were presented on a computer screen and participants responded with either a power or precision grip depending on whether the object was e.g. natural or manufactured. These responses could be compatible (precision grip for pencil) or incompatible (precision grip for a hammer) with the object seen on the monitor and object grasp compatibility significantly decreased the time to initiate the grasp (Tucker & Ellis, 2001). According to the study by Tucker and Ellis (2004), it seems possible that even after a brief presentation, the cue object is fully processed and has the ability to cause the object affordance compatibility. Therefore, merely viewing the cue object longer, by having a preview before the onset of the movement, does not mean that the identity of cue object is then fully processed. We suggest that the cue object can be briefly presented and still generate visuomotor priming, as long as the features of the cue object are processed that cause visuomotor priming.

Glass type influence. Additionally to the visuomotor priming effect, we found an influence of the glass type. Specifically, the pick-and-place movement was faster when the target glass was a beer-glass compared to the wine glass (all MT1 and MT2, except MT1 in Experiment 2). At the same time, the initiation times did not differ between beer and wine glasses. The finding that beer glasses result in faster movement times is not surprising, since grasping a wine glass requires a more fine-tuned motor control of the participant than do water glasses (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987).

Taken together, the results of the present chapter showed visuomotor priming effects not to occur automatically and are not simply stronger the longer the cue object is presented. It is even insufficient if the cue object is task relevant and thus attracts attention to cause an automatic potentiation of the action. Rather, those properties of the cue object, which can be congruent or incongruent have to be processed deep enough before they can generate the visuomotor priming effect. The identity of the cue object was in the present chapter not task-relevant and therefore only weakly processed. If however, the identity of the cue object was made relevant, visuomotor priming effects occurred. This effect was shown to be independent of the time the cue was visible. Additionally, the effects of the present chapter can be transferred to natural settings as well with real objects as cues and target objects. Therefore it can be suggested that visuomotor priming does not occur automatically by merely viewing objects, but the relevant feature of the cue object that can be congruent or incongruent, has to be task-relevant as well. In the following *General Discussion*, the findings of the present thesis are discussed.

CHAPTER VI

General Discussion

General Discussion

The present thesis was aimed at investigating the cognitive architecture of perceptual influences on action. Specifically, the thesis addressed the issue of movement planning and execution being influenced by (i) saliency maps, (ii) location-unspecific memory and (iii) the way objects are processed. The evidence existing currently in the literature has hitherto failed to address these issues specifically, but rather focused on the broader context of perception-action interactions. Therefore, this thesis has sought to fill this gap in the literature in order to illuminate the details of the coupling between perception and action. In the following discussion, the results of the present thesis are integrated into the current state of the art literature and the coherence of the studies in the present thesis is illustrated.

Salience maps and motor actions. Salience maps and its influence on behavior have until now only been investigated within the context of attention and eye movements (see Fecteau & Munoz, 2006 for a review), but surprisingly not for movement planning and execution. Chapter 2 and 3 of the present thesis addressed the question how salience and the salience map affect action. The salience map integrates visual information by summing up visual signals into different feature maps before being integrated into a master saliency map (e.g., Itti & Koch, 2001). The master salience map then signals the most relevant or most interesting location in visual space which can be used to guide attention or an eye movement to that location for further processing (e.g., Goldberg, et al., 2006). Research so far has been focused on the influence of the salience map on the guidance of attention and eye movements with only a hint in the literature that signals from the FEF (and therefore the salience map) might be motor-unspecific (Thompson & Bichot, 2005). Therefore the main goal of Chapter 2 was to investigate four different well-known effects within the visual search paradigm that have been found to be influenced by the salience map. The purpose of Chapter 2 was to investigate whether the latencies of manual pointing movements to search targets in a visual search display would be modulated by the same manipulations of salience. Clear evidence was provided in Chapter 2 by showing qualitatively similar patterns of these well-known effects such that movement initiation times were slower for low- than for high-contrast targets, for cross-trial changes of the target-defining dimension than for repetitions, for neutral compared to valid pre-cues of the upcoming dimension and finally for targets defined in a single dimension compared to a redundant target defined in two dimensions. The results of Chapter 2 therefore provide clear evidence that signals from the salience map are able to influence movement planning. Further whether the salience map has the ability to affect movement execution was investigated in Chapter 3.

Visual information has been found to influence movement execution (e.g., Ma-Wyatt & McKee, 2006), independently of the movement planning process. In Chapter 2, it was shown that movement latencies are modulated by salience, but is this salience-dependent modulation in movement execution still visible? In a series of experiments with a similar experimental setup than in Chapter 2, it was shown that visual salience has the ability to guide movement execution with faster movement times for high compared to low feature-contrast targets by controlling that these effects have its origin at the movement execution stage.

In light of these findings, I recommend that visually guided reaching movements (movement initiation as well as movement execution) be integrated into the construct of a salience map in recognition of its functional relevance in guiding not just perception, but action as well. One possible mechanism how the salience map and actions such as pointing movements are interacting is through the PPC. The PPC is a structure in the brain that is known to signal salient locations in visual space and is relevant for the programming and initiation of actions (e.g., Constantinidis & Steinmetz, 2005; Snyder, Batista, &

Andersen, 1997). In this framework, all possible action goals which are in the present thesis possible locations of targets and distracters, are represented on the salience map with a bias toward the most salient location in visual space. This biasing mechanism to the most salient location is stronger, the more salient the signal is compared to its surrounding elements. In light of the present thesis, highly salient targets produced faster movement initiation times than less salient targets (see Chapter 2), which reflects the strength of the bias (confidence) towards one location. As the salience map is not a static, but a continuous process depending on the visual input (e.g., Dombrowe, Olivers, & Donk, 2010), this might reflect the variations in the time to execute the movement (Chapter 3) according to the strength of visual salience of the target. More evidence in favor of this bias is coming from endpoint variations (Chapter 3), there was more variation in the endpoint distribution the less salient the target was compared to the distracters. The more salient a target is compared to its surrounding distracters, the more confident one can act towards that target resulting in faster and more precise actions. The described mechanism for selecting potential actions could explain the results of Chapter 2 and 3 and should be considered in future versions of salience map constructs.

Memory in grasping movements. In Chapter 4, the differential effects of memory on grasping behavior were investigated with evidence that objects are stored in memory in a location-unspecific manner. Previous research has conceptualized visual memory processing in motor actions as a single, unified entity, excluding the possibility that location information and object information are stored in separate memory systems (e.g., Hesse & Franz, 2009). In Chapter 4, participants grasped two different kinds of glasses from two different starting positions and placed it onto a box. The two different glasses and the position of the glass were either the same or varied between trials. Given the results obtained in Chapter 4, future research on visual memory and motor action should differentiate between these different memory systems and their different decay rates. One possible mechanism why objects are stored in a different way than its proper location could be that object features usually stay constant throughout time, while the location of the object or the actor changes its position more frequently. It can only be speculated whether location-specific memory effects could have been observed when the interval between two trials was shorter (at least 6.5 sec between two trials), since there have been findings that the position of the target in the last trial influences the behavior of the current trial (e.g., Chapman et al., 2010). The main difference between the findings of the study by Chapman et al. and the findings from Chapter 4 with no memory effects for spatial location was the time between two trials with a maximum intertrial interval of 2750 ms compared to the study of Chapter 4 with at least 6.5 sec. Future research in that area is needed to distinguish between these two separate memory systems and explore the details and differences between them. For example one could manipulate both location and feature of the object with variations in the time between two trials. With such an experiment, one is able to investigate the different decay rates and interactions between these two memory systems. To sum up, the results of Chapter 4 indicate that memory traces responsible for feature-based intertrial effects are location unspecific and have the ability to affect subsequent grasping movements even when they differ in spatial parameters.

Specific visuomotor priming effects. The results of Chapter 5 contradict previous research on visuomotor priming (e.g., Craighero, et al., 1996; Grèzes, Tucker, Armony, Ellis, & Passingham, 2003) in a way that visuomotor priming is not automatic, but rather the relevant feature of the cued object (i.e., the congruent or incongruent feature) must be task-relevant if it is to generate visuomotor priming. So far, the experimental setups using the visuomotor priming paradigms did not allow to differentiate between automatic visuomotor priming and non-automatic visuomotor priming. In a classical study, automatic visuomotor priming was visible under circumstances when the feature that was primed was at the same time task relevant (e.g., Craighero, et al., 1996). In the study by

Craighero et al., the task consisted of simple bars oriented to the left or to the right with no other variations. This means that the orientation of the bar was the only feature that was manipulated in the task and therefore the only feature in the task that was relevant to solve the task. That is the reason why previous visuomotor priming studies claimed that visuomotor priming was an automatic process (e.g., Craighero et al., 1996; Craighero, et al., 1999) with mere exposure of the objects already affording an action. In Chapter 5, a similar setup was used as in Chapter 4 with two different glasses as action and as cue objects in a pick-and-place task. The factor cue exposure time (short vs. long) was crossed with relevance of cue identity in a secondary memory task (relevant vs. irrelevant). In Chapter 5, it could be shown that not the time available to view the object (with or without a preview condition) before initiating the response was responsible for visuomotor priming. However the manipulation responsible for visuomotor priming was an additional task, in which it was necessary to remember the identity of the cue and report it after the trial. A similar manipulation was implemented in a different paradigm (automatic imitation), at which participants' attention was directed to the relevant feature of hand and automatic imitation effects were only visible when attention was directed to the relevant feature of the hand (Chong et al., 2009). With respect to visuomotor priming and automatic imitation, Chapter 5 shed new light in how human beings process visual information and how motor representations are formed in the brain. Generalizing this to everyday human behavior this means that not all viewed objects produce action or object affordances but only those that are relevant for the current behavior and goals of the actor.

Processes affecting action. In this section the relation between the four different studies (Chapter 2 to Chapter 5) is described and identified. On the most general level of explanation, the studies in the present thesis were investigating perceptual effects on action. As measures for the action, movement planning and execution of pointing and grasping movements were analyzed. The measured effects in the present thesis can be summarized under implicit memory processes with dimensional weighting and the pre-cueing of the relevant dimension (Chapter 2), history effects in grasping movements (Chapter 4) and visuomotor priming in grasping movements (Chapter 5). The salience map, a theoretical construct representing visual salience, links Chapters 2 and 3 with one targeting the movement planning process (Chapter 2) and the other the movement execution process (Chapter 3). This section described the relationship between the different studies in the present thesis with motor actions being used to investigate cognitive processes.

Generalizability. The results of the present thesis contributed substantially to the generalizability with respect to previous findings. In detail, Chapter 1 and 2 provided evidence that the output of the salience map is motor-unspecific and can not only be used to guide attention and eye movements, but also visually guided reaching movements. Chapter 4 and 5 did not only provide new insights into memory mechanisms and visuomotor priming in motor action, but the results can be generalized to natural settings with natural objects used in everyday life. In most previous studies examining grasping behavior, relevant stimuli were presented on computer displays and participants had to grasp vertically oriented rods (e.g., Chong et al., 2009) or simple bars (e.g., Hesse & Franz, 2009). However Chapters 4 and 5 employed natural objects (wine and water glasses) in conjunction with a realistic non-speeded pick-and-place task. The naturalistic characteristic of these designs suggests that the phenomena uncovered about the human visual memory mechanisms and visuomotor priming can be generalized to everyday situations in which movements are not accomplished within milliseconds but usually within seconds. In summary, the present thesis investigated phenomena that can now be generalized to behaviors in everyday life and saliency signals guiding not only visual attention and eye movements but also motor actions.

Perception-action coupling. To conclude, the results of the present studies show how the perceptual and the action system are coupled by demonstrating that movement planning and movement execution are influenced by salience maps, memory processes and the way objects are perceived. Future considerations about the salience map should take into account that signals from the salience map cannot only be accessed by the attentional and saccadic system but are also able to guide visually guided movements. The process how object information is stored in memory during visually guided grasping movements was clarified in that object features are stored in memory independent of its location from the previous trial. Additionally, in order to generate the visuomotor priming effect in visually guided grasping movements it is insufficient to merely view the object to produce visuomotor priming, but the relevant feature of the object has to be task relevant as well. In more general terms, it can be summed up that the primate perception-action system is adaptive and flexible to current and preceding perceptual and motor events.

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Appendix

Appendix A: Supplementary Data

ANOVA interaction results for RTs, MT1 and MT2 and total time (TT)

Factor	F	p	F	p	F	p	F	p
	RT		MT		MT2		TT	
object transition x position transition	0.58	.46	3.98	.06	0.11	.74	0.16	.70
object transition x target object	0.45	.51	0.23	.64	0.43	.52	1.37	.26
object transition x object location	0.74	.40	0.00	.98	0.07	.80	0.05	.83
position transition x target object	3.30	.09	0.01	.93	1.00	.76	1.40	.25
position transition x object location	0.00	.98	2.77	.11	0.48	.50	0.04	.84
target object x object location	0.36	.56	3.76	.07	5.22	.03	8.66	.01
object transition x position transition x target object	0.72	.41	0.02	.89	2.81	.11	0.45	.51
object transition x position transition x object location	0.59	.45	0.41	.53	1.58	.22	0.17	.69
Object transition x target object x object location	0.03	.86	0.32	.58	1.11	.30	0.80	.38
Position transition x target object x object location	0.24	.63	0.07	.80	0.39	.54	0.18	.68
object transition x position transition x target object x object location	0.96	.34	1.52	.23	0.00	.98	0.01	.93

All results with 19 degrees of freedom and exact p values.

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Curriculum Vitae

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Education

03/2012 - to date	**Post-Doctoral researcher**, Tel Aviv University, Israel
04/2009 - to date	**Ph.D. student** at the chair of General and Experimental Psychology, Ludwig-Maximilians Universität, München supervised by Prof. Hermann Müller and Dr. Michael Zehetleitner and participant of the Graduate School of Systemic Neuroscience, LMU, München
05/2010 - 06/2010	**Research project at the Harvard University**, Boston, USA
10/2007 - 03/2009	**Master of Science in Neuro-Cognitive Psychology**, Ludwig-Maximilians University, München (Elite masters program of the elite network bavaria)
10/2004 - 07/2007	**Bachelor of Science in Psychology**, University of Fribourg, Switzerland

Teaching experience

- 10/2011 - 03/2012: Seminar: scientific working techniques
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- 10/2010 - 03/2011: Seminar: scientific working techniques
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- 10/2009 - 03/2010: Tutorial: Classical psychological methods
- 10/2006 - 08/2007: Tutorial: Computer based data analysis
- 10/2005 - 03/2006: Seminar: scientific working techniques

Prices and awards

- Participant of the Autumn School für "Cognitive, Affective, and Nociceptive Functioning of the Anterior Cingulate Cortex" in the Castle Oppurg, Germany (11/2010)
- Participant of the Summer School for “Computational Vision” in the Castle Rauischholzhausen, Germany (08/2009)
- Finalist – Student Robot Design Competition ACM SIGCHI/SIGART, Amsterdam, Netherlands (03/2008)
- Gallup Travel Fellowship, 6th Gallup Positive Psychology Summit (10/2007), Washington, D.C., USA

Publications

Zehetleitner, M., Hegenloh, M., & Müller, H. J. (2011). Visually guided pointing movements are driven by the salience map. *Journal of Vision, 11(1)*, 1–18.

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Samson, A. C. & Hegenloh, M. (2010). Structural stimulus properties affect humor processing in individuals with Asperger syndrome. *Journal of Autism and Developmental Disorders, 40 (4),* 438-447.

Conference attendances

German Neurophysiology PhD Meeting, Tübingen, Germany (2011), Vision Science Society, Naples, USA (2010, 2009), European Conference on Visual Perception, Regensburg, Germany (2009), Swiss Psychological Society, Neuchatel & Zürich, Switzerland (2009, 2007), Visual Search Symposium, Fribourg, Switzerland (2009), Tagung experimentell arbeitender Psychologen, Marburg, Germany (2008), ACM SIGCHI/SIGART, Amsterdam, Netherlands (2008), Gallup International Positive Psychology Summit, Washington D.C., USA (2007), National Conference for Psychology students, Le Noirmont & Vaumarcus, Switzerland (2006, 2007)

Eidesstattliche Versicherung

Ich versichere hiermit, dass die vorgelegte Dissertation von mir selbständig und nur unter Verwendung der angegebenen Hilfsmittel angefertigt wurde.

Michael Hegenloh

München, Juni 2012