Visual Selection of Multiple Movement Goals

Inaugural-Dissertation

zur Erlangung des Doktorgrades der Philosophie an der
Ludwig–Maximilians–Universität München

vorgelegt von

Daniel Baldauf

Im Oktober 2007

Tag der mündlichen Prüfung: 15. Januar 2008

Prüfer:

Prof. Dr. Heiner Deubel, Department für Psychologie, LMU

Prof. Dr. Hermann Müller, Department für Psychologie, LMU

Prof. Dr. Benedikt Grothe, Department für Biologie, LMU

Contents

1 Overview and Theoretical Framework

1.1 Vision is purposive and selective

When inspecting a visual scene, viewers selectively process only certain parts or aspects in full detail. Most of the input is filtered out and discarded in order to economize the use of cognitive resources (Ullman, 1984). Visual perception is therefore not a uniformly detailed representation of all stimuli in the scene. What we see is crucially determined by our current interests, by what we do or intend to do. Such top-down information about the current task (or immediate plans) has a strong impact on how the various parts of the brain deal with sensory input. Compelling evidence for this was provided, for instance, by studies that investigated observers' sensitivity to notice changes in their field of view. Wallis & Bülthoff (2000) demonstrated in a simulated driving environment that drivers and passengers have different sensitivities to artificial changes in the scene. Triesch and colleagues asked the participants in their study to sort objects in a virtual reality (Triesch, Ballard, Hayhoe & Sullivan, 2003). The subjects often exhibited an astonishing inability to detect significant, salient changes that sometimes happened right in their line of view or even to the objects they were holding in their hands. On the contrary, they did not miss more subtle changes of objects in the scene that were immediately relevant for the task at exactly the point in time when the changes occurred (see also Droll, Hayhoe, Triesch & Sullivan, 2005).

Vision is not a passive processing of available information. Rather, vision has an active nature and is flexibly adjusted to what is relevant for the ongoing behaviour (see also Findlay & Gilchrist, 2005). Various studies documented the way humans use specific aspects of the visual information by continuously reorienting their eyes to task-related locations in everyday tasks, such as walking (Jovancevic et al., 2006), steering a car (Land & Lee, 1994; Land, 1998), preparing a cup of tea (Land, Mennie & Rusted, 1999) or a butter-jelly sandwich (Hayhoe, Shrivastava, Mruczek & Pelz, 2003). Most importantly, however, visual input is not only selected by eye movements, that - of course – determine which part of the surrounding visual environment can enter the processing as a 2-D retinal image. Also covertly attending to an object in the periphery facilitates visual perception at this location and allows for faster detection (e.g., Posner, 1980; Shulman et al., 1979) by enhancing visual signals (e.g., Mangun & Hillyard, 1987, 1988, 1990, 1991; Luck & Hillyard, 1995; Luck, Hillyard, Mouloua, Woldorff, Clark & Hawkins, 1994; Hawkins, Hillyard, Luck, Mouloua, Downing & Woodward, 1990; Henderson, 1996; Hillyard & Munte, 1984; Michie, Bearpark, Crawford, & Glue, 1987) and improving contrast sensitivity (Pestillo & Carrasco, 2005; Carrasco, Penpeci–Talgar & Eckstein, 2000). This is often a prerequisite for all features of an object (which are processed in different visual modules) to be successfully integrate and to be bound into object files (Treisman & Gelade, 1980) thus allowing for an accurate identification of objects (Eriksen & Hoffman, 1972; Müller & Rabbitt, 1989; LaBerge & Brown, 1989). Further, the attentional selection often determines which objects access the visual short-term memory (Duncan, 1984; Bundesen, 1990) and later guide behaviour.

Reorienting of visual attention (covertly or overtly) is not always a voluntary act but often an implicit process that may occur without being noticed by the viewer. Perception is permanently influenced by top-down signals and embedded in some context of behavioural relevance like interests, plans, or intentions.

Prominently, most of the movements humans perform are planned on the basis of visual input. This is not only true for complex navigations as operating machines or manipulating objects. Also effortless and seemingly simple movements like manually grasping an object (Castiello, 1996) or reorienting the eyes several times a second (Yarbus, 1967) have to be prepared by analyzing the visual input and identifying regions of primary interest. The central nervous system needs to transform only relevant visual information into neural commands for a given effector system in order to visually guide any kind of action. Information about objects that are irrelevant for the task has to be decoupled from controlling actions (Castiello, 1996; Allport, 1987), i.e. ignored or inhibited, in order not to distract or to interfere with the movement goals (Sheliga, Riggio & Rizzolatti, 1994; Tipper, Howard & Jackson, 1997; Tipper et al., 1994; Tipper, Lortie & Baylis, 1992). Task- dependent selection is therefore one of the first computational steps in the preparation of goal-directed movements. Allport named this function of visual attention 'attention-for-action' (Allport, 1987). The preferred visual processing of movement-relevant information is a prerequisite for the accurate computation of movement parameters like the direction or the amplitude of an intended reach (parameter specification, Neumann, 1987). The premotor theory of attention (Rizzolatti, Riggio & Sheliga, 1994; Rizzolatti, Riggio, Dascola & Umilta, 1987) postulates a tight functional coupling between attention and motor planning, stating that "the system that controls action is the same system that controls spatial attention" (Rizzolatti, Riggio & Sheliga, 1994, p.256).

1.2 Selection-for-saccades

The hypothesis that goal-directed movements are preceded by attention shifts to movement-relevant positions has been extensively studied in the context of oculomotor control. In complex visual scenes, the selection-for-saccades is a crucial precondition for accurately directing eye-movements to the objects of interest because the oculomotoric system has to know in advance which of all the available objects in the scene is the effective target for the next fixation. Most of the studies investigated these dependencies in controlled laboratory settings. Remington (1980) was among the first who found attentional facilitation at the intended saccade goals. He showed that before the saccade is executed the detection of briefly flashed stimuli at the saccade goal are facilitated, compared to the detection performance at the same location when no saccade is planned. Interestingly, the performance at the intended target location was even slightly better than close to the eye fixation, although the fixation point was foveated. Shepherd and colleagues (Shepherd et al., 1986) also used a simple detection task to measure the deployment of visual attention in the field. They instructed participants to make a saccade to a centrally cued box to the right or to the left of the fixation point. A visual transient was briefly presented just before the saccade and the subjects had to press a key as soon as they detected the stimulus. The manual reaction times were shorter if the transient was flashed at the intended saccade goal suggesting that processing at the goal location was speeded by visual attention.

Kowler and colleagues (Kowler et al., 1995) provided further evidence in favour of this notion in a study with a dual-task paradigm. In their experimental task they combined a prioritized movement task with a secondary perceptual task. They presented displays containing eight pre-masks on a circular array. The participants were instructed to make a saccade from the central fixation point to the item indicated by a central arrow cue as soon as the cue appeared. Simultaneously with the onset of the cue, the mask elements changed into letters, which were again masked 200 ms later. After the instructed saccade was executed the participants responded by pressing a respective key which letter had been presented (forced-choice task). The results of this experiment showed that the letter report accuracy was considerably higher for letters that had appeared at the saccade target as compared to letters at movement –irrelevant locations. This demonstrates that during the preparation of a single saccade the ability to visually discriminate objects is selectively enhanced at the intended goal position. In a second experiment the authors attempted to force a dissociation between saccade preparation and attention. In the ‘fixed report’ condition (see Kowler et al., 1995, Exp. 2) the participants were instructed to try to identify a letter that was presented at the same position in each trial simultaneously with the movement cue onset. An important result was that participants could do so, but only at the cost of prolonged saccade latencies and loss of saccade accuracy. Therefore, perceptual attention could not be completely dissociated from the saccade goal.

The findings were replicated by several following studies (Hoffman & Subramaniam, 1995; Deubel, Schneider & Paprotta, 1996; Schneider & Deubel, 2002). In the task of Deubel and Schneider (1996) the participants were first shown string-like arrays of differently coloured premask elements to the left and to the right of the central fixation point. A central colour cue was presented, which indicated one of the items in the strings as the next saccade goal. As soon as the central cue was removed, the participants had to saccade to the previously cued location. Shortly after the cue removal (Go-signal) but before the saccade onset, a discrimination target (resembling the symbol ’E’ vs. ’∃’) appeared at a random location in the string. All the other string elements changed simultaneously into irrelevant distractors. After 120 ms presentation time and still before the onset of the instructed saccade all elements were removed. At the end of each trial the subjects had to report the identity of the discrimination target (2AFC). Again, the results showed that the discrimination accuracy was significantly higher if the discrimination target was presented at the saccade goal compared to those trials, in which it appeared at the adjoining positions. The enhanced processing of the saccade goal was also found in another version of the experiment, in which the participants knew in advance the location of the discrimination target. This suggests that in this experimental paradigm it is not possible to covertly shift attention to a location of interest while preparing a saccade to a different location. Rather, the coupling between saccade preparation and covert shifts of visual attention is mandatory. Paprotta and colleagues (Paprotta, Deubel & Schneider, 1999) improved the experimental setup by adding a post-mask after the presentation of the critical discrimination targets and replicated the findings.

Novel evidence for attentional shifts before saccades comes from a study by Van der Stigchel & Theeuwes (2005) who investigated the selection of movement goals by analyzing event related potentials (ERPs) in the human electroencephalogram before the execution of an eye-movement. In their paradigm two peripheral objects were cued by central arrows. A red arrow cued the later saccade goal, an equiluminant green arrow indicated a distractor object that had to be ignored. The analysis of the ERPs induced by the onset of the arrows revealed that the preparation of a saccadic response to the target elicited an early directing attention negativity (EDAN) as well as an anterior directing attention negativity – both over the contralateral hemisphere. This result is remarkable, taken into consideration that previous studies, which did not involve eye-movement responses, interpreted these components as related to covert allocation of attention (Hopf & Mangun, 2000; Nobre, Sebestyen & Miniussi, 2000; Eimer, Van Velzen & Driver, 2002; Eimer, Van Velzen, Forster & Driver, 2003; Slagter, Kok, Mol & Kenemans, 2005; Green, Teder-Salejarvi & McDonald, 2005). The

EEG-recordings further hint to the existence of a new component over the right hemisphere, which may be related to the inhibition of a distracting object (see, e.g., Tipper, Howard & Jackson, 1997).

1.3 Attention before reaches and grasping

The term selection-for-action is not conceptually limited to the relationship between attention and the oculomotor system. Allport (1987) pointed out that the selection of action goals is a very general term that equally applies to eye-movements as well as to reaching and grasping movements or even to the hunting strategies of a predator, All these instances share a common problem, namely to guide an action to one goal, even though the brain encodes multiple objects in parallel including those that are currently not of interest (Allport, 1987, p.396). Accordingly, several studies empirically investigated the process of target selection in the context of various actions humans perform, especially the control of hand actions. For instance, reach and grasp movements have been studied in conditions with distracting objects that are known to attract visual attention. Tipper and colleagues investigated the effect of a visual distractor on the kinematics of goal-directed reaching movements (Tipper, Lortie & Baylis, 1992). The distractor prolonged the latency of a reaching movement only if it had a certain spatial relationship to the goal. For example, the irrelevant stimulus had an effect on the movement preparation if it appeared between the starting position and the goal, whereas it did not hamper the movement if it was presented beyond the reach goal. Other studies found similar interference effects from non-targets on the preparation of reach-to-grasp or pointing movements (Jackson, Jackson & Rosicky, 1995; Howard & Tipper, 1997; Tipper, Howard & Jackson, 1997; Tipper, Howard & Houghton, 1998). Interestingly, such non-targets did not interfere with the preparation of reach-to-grasp movements if their location and identity was known in advance or if they were stationary present and therefore did not need to be online computed (e.g., Castiello, 1996; Bonfiglioni & Castiello, 1998). Castiello and colleagues (Castiello, 1996) developed a dual-task, in which subjects had to grasp an object while counting the number of times a distractor object was illuminated by a spotlight. They found that the size of the distractor had an effect on the grip aperture of the hand. Small distractors lead to a decrease of the grip aperture amplitude and big distractor increased the maximal aperture. In an experiment by Bonfiglioni and Castiello (1998) participants had to covertly monitor a moving distractor in the periphery and simultaneously grasp a target object. The covert allocation of attention to the distractor affected the transport component (e.g., the peak velocity of the hand) of the reach-to-grasp movement, but not the grasp-component, which adjusts the hand aperture to the size of the target. Possibly there was no effect on the grasp component because distractor and target object were similarly sized. In a follow-up study, Kritikos and colleagues (Kritikos, Bennett, Dunai & Castiello, 2000) also manipulated the size of the distractor and found that distractor objects again interfered with the grasp-component of a planned reach, even if both objects differed in size.

In all these studies the programming of the reach-to-grasp movement was influenced by covertly attended information in the visual field. Castiello (1998) developed a task, in which the participants had to grasp an object while attending to a distractor object for a secondary detection task. The distractor could be either two- or three-dimensional. Attending to the two-dimensional distractor did not interfere with the grasp component of the movement. However, when the participants had to attend a three-dimensional distractor while grasping for the goal object the grasping component, i.e. the adjustment of the hand aperture, was significantly distorted. For the grasp-component, interference from attending to irrelevant objects seems to be limited to conditions, in which the distractor and the goal object share task-relevant properties, like dimensionality.

Deubel, Shimojo & Paprotta (1997) used the line motion illusion to further test test the dynamics of attention before manual pointing movements. The illusionary line motion describes the phenomenon that a flashed line segment appears to the observer to expand from the end of the line, where he or she covertly attends to (see, e.g., Hikosaka et al., 1993; Titchener, 1908). In the study of Deubel et al., two objects were presented to the participant in the periphery of the visual field. As soon as one of them was exogenously cued, the subject had to execute a pointing movement to the opposite location. During movement preparation, a line segment was briefly flashed between both positions. After each trial the participant reported, from which end of the segment they thought the line had started to expand. By varying the onset of the line segment in time, the authors could sample the shift of attention to various positions in the field. Segments that were flashed during the first 200 ms after the cue onset appeared to the observer as expanding from the cued end of the line. If, however, the segment was flashed right before the movement started, i.e. 200-400 ms after the cue onset, observers had more often the impression that the line expanded from the opposite end, the movement goal. The authors concluded that attention was first automatically attracted by the exogenous cue and then reoriented to the opposite location in order to prepare for an accurate reach.

Converging evidence for a coupling between visual attention and the preparation of hand movements was provided by studies that directly tested for perceptual facilitation at the intended movement goal. Deubel, Schneider and Paprotta (1998; 1996b) modified the paradigm of Deubel et al. (1996) and instructed participants – without breaking ccentral eye fixation - to execute a manual pointing movement towards a cued element in a horizontal arrangement. Between the cue onset and the movement start a target letter was flashed at any of the element positions while distractors were presented at all other locations. Discrimination performances was higher if the target letter was presented at the same position as the movement had to be prepared to. This is direct evidence for visual attention to be covertly shifted to the intended movement goal before the onset of the manual reach thus facilitating perception at this locations as compared to other, movement-irrelevant locations. The results were replicated in a study by Paprotta and colleagues (Paprotta, Deubel & Schneider, 1999) by using a modified experimental setup, in which pointing movements had to be executed in different directions towards elements that were arranged on a circular array.

In another study, Schiegg and colleagues (Schiegg, Deubel & Schneider, 2003) investigated the grasping of a three-dimensional object. In their experiment, a primary movement task was combined with a secondary perceptual task in order to measure the deployment of attention during action preparation. The participants had to grasp a cross-like object either with their left or right hands touching the ends of either the left- or right-tilted part of the cross. The authors then analyzed the discrimination performance for target letters presented at various positions on the object before the movement onset. Right before participants reached for the object, the intended points of application for the thumb and index finger were preferentially processed over other parts of the same object. Humphreys and colleagues recently came to a similar conclusion (Humphreys, Riddoch, Linnell, Punt, Edwards & Wing, 2005) by analyzing the identification of objects that were perceptually grouped together. In one condition, the subjects only had to identify a cued part of the grouped configuration, and the results showed that the perceptual selection spread over the whole configuration allowing the identification of all component parts. This object-based benefit, however, was eliminated in second condition where the participants had to direct a hand movement to one part of the object. Here, identification performance was only improved for the object part, towards which the action was directed.

Additional support for a functional coupling of movement plans and selective visual processing comes from a series of patient studies (Riddoch, Humphreys, Edwards, Baker & Wilson, 2003). The patients had uni-lateral neglect following lesions to the parietal lobe and showed the syndrome of visual extinction, i.e. impairments to perceive a stimulus in the contralateral side if and only if another stimulus appears on the ipsilateral side (e.g., Karnath, 1988). The authors presented a pair of objects - one in each hemifield - that were commonly used together, e.g.,a bottle of wine and a corkscrew. In two different conditions they manipulated whether the two objects appeared in the appropriate spatial relation to be used together (e.g., a corkscrew in the upper left hemifield going into the top of a wine bottle in the lower right hemifield). When the stimuli were arranged in such correct constellations extinction was decreased and both objects could be significantly better identified as compared to trials, when the same objects were placed in incorrect positions for action (e.g., the corkscrew in the lower left quadrant going into the bottom of the bottle in the upper right quadrant). A control experiment ensured that the effect was not due to visual familiarity of the objects. The perceptual selection of objects - a prerequisite for their identification - is sensitive to action relations between objects in the field.

1.4 Neurophysiology of attention

Spatial selective attention modulates early stages in the processing of incoming visual information via feedback connections. At already the level of the lateral geniculate nucleus attentional shifts lead to an increased baseline activity in neurons with receptive fields in the attended portion of the visual field (O'Connor, Fukui, Pinsk, & Kastner, 2002). Additionally to these baseline shifts, attentional top-down signals selectively amplify visual responses to preferred stimuli inside of a cell's receptive field (Li, Piech & Gilbert, 2004; Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999). Attention modulates the response patterns of neural populations throughout almost all hierarchal levels of the visual system. Top-down modulations have been found by various studies in areas V1 (Li, Piech & Gilbert, 2004; Christ, Li & Gilbert, 2001; Ito & Gilbert, 1999; Roelfsema, Lamme & Spekreljse, 1998; Motter, 1993), V2 and V4 (Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999; Corbetta, Kincade, Ollinger, McAvoy & Shulman, 2000; Motter, 1994; Moran & Desimone, 1985; Desimone, Moran & Spitzer, 1989; McAdams & Maunsell, 1997), MT and MST (Treue & Maunsell, 1996), IT and TEO (Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999; Desimone, Moran & Spitzer, 1989). It appears that top-down signals of spatial selection processes permanently influence all levels of visual processing in parallel and access processes for object and feature analysis (Corbetta & Shulman, 1998).

Desimone and colleagues refined the understanding of attentional facilitation by providing evidence in favor of a biased-competition model. This model claims that the neural representations of objects compete with each other (Desimone & Duncan, 1995). Instead of just enhancing selected parts of the visual field (by baseline shifts or by modulating the response to presented stimuli) the neural representations of various objects in the field inhibit each other reciprocally. A stronger activity for one representation implies a reduction in activity for other representations. The neural theory of visual attention (NTVA) by Bundesen and colleagues (Bundesen, Habekost & Kyllingsbaeck, 2005) is a mathematical model that describes - on the basis of a biased-competition account - how attentional weights are assigned to various objects in the field. The bigger the relative attentional weight that is given to an object, the more computational resources deal with the analysis of its features.

Sources of attentional top-down signals. The studies referenced above describe sites throughout the ventral path of the visual system in the primate brain, which are involved in the analysis of visual input and are modulated by the attentional state of the organism. This leads to the really important question where the modulating attentional top-down signals origin, the sources of attentional facilitation (see Corbetta & Shulman, 2002). The electrophysiological recording of single units in behaving monkeys provided invaluable insights into the function of a fronto-parietal network. Interestingly, it has become evident that the mechanisms underlying the deployment of attention share common structures with areas that mediate the programming of movements (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975).

Parietal areas. Single cell recordings in behaving monkeys indicated that activations in various parts of the parietal cortex are associated with shifts of covert attention (Corbetta & Shulman, 2002; Colby & Goldberg, 1999; Colby, Duhamel & Goldberg, 1996; Robinson, Bowman & Kertzman, 1995; Steinmetz & Constantinidis, 1995; Bushnell, Goldberg & Robinson, 1981). This is not too surprising given the fact that damages to parietal regions in humans are known to produce severe problems in the orienting of spatial attention (Balint, 1909; Heilman, Watson & Valenstein, 1985; DeRenzi, 1982; Mesulam, 1990). Furthermore, the single-unit recordings are supplemented by an extensive collection of fMRI studies in humans that used various experimental paradigms to manipulate the focus of covert attention (Kanvisher & Wojciulik, 2000; Corbetta, Shulman, Miezin & Petersen, 1995; Corbetta, Shulman, Conturo, Snyder, Akbudak, Petersen & Raichle, 1997; Heinze, Luck, Munte, Gös, Mangun & Hillyard, 1994; Woldroff, Fox, Matzke, Veeraswamy, Jerabek & Martin, 1995; Nobre, Sebestyen, Gitelman, Mesulam, Frackowiack & Frith, 1997; Vandenberghe, Dupont, Debruyn, Bormans, Michiels, Mortelmans & Orban, 1996; Vandenberghe, Duncan, Dupont, Ward, Poline, Bormans, Michiels, Mortelmans & Orban, 1997). Most of them found a considerable overlap of activation along the intrapariteal sulcus in the posterior parietal cortex.

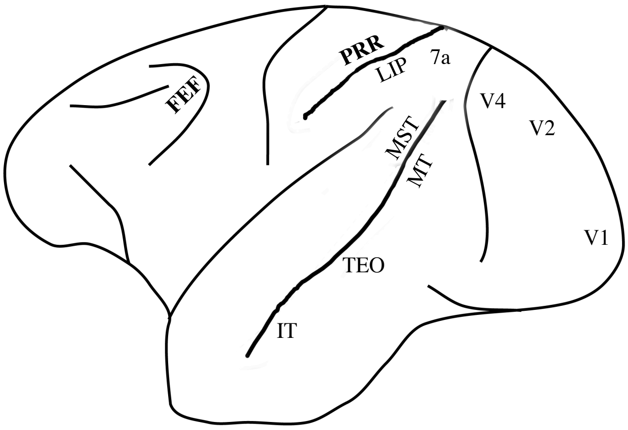


Figure 1.1: Schematic side view of the macaque brain. Depicted are several important structures involved in the processing of visual information. Activity in most of the sites were shown to be modulated by selective attention. Prominent sources of spatially selective top-down signals are part of a fronto-parietal attention network (bold labeled structures). Abbreviations: FEF: frontal eye field, PRR: parietal reach region, LIP: lateral parietal area, MT: medial-temporal, TEO: temporal-occipital, IT: inferior-temporal. PRR and LIP are deep structures at the medial and lateral bank of the intraparietal sulcus (IPS); MST and MT are located inside the superior-temporal sulcus (STS).

A more systematic mapping of the posterior parietal cortex (PPC) provided a detailed image of the functions of discrete neural subpopulations for the preparation of movements. It has been shown that neurons in different sections of the PPC prospectively encode movement goals in an eye-centred frame of reference (Batista, Buneo, Snyder, & Andersen, 1999) even during extended memory periods in the absence of direct sensory input. Further, it turned out that the external space is represented in parallel in various spatial pragmatic maps of PPC. Each of these maps encodes movement goals for a specific effector system (Scherberger & Andersen, 2007; Andersen & Buneo, 2002; Calton, Dickinson & Snyder , 2002; Snyder, Batista & Andersen, 2000;

Andersen, Snyder, Bradley & Xing, 1997; Snyder, Batista & Andersen, 1997; Graziano & Gross, 1994). Such findings led to the hypothesis that movement intentions (i.e. where to move which effector) are encoded in subdivisions of PPC. In an experiment by Cui & Andersen (2007) for example, the intention to reach the arm to peripheral goal position activated the parietal reach region (PRR) in the medial bank of the intraparietal sulcus, but not the lateral intraparietal area (LIP). Vice versa, the intention to make an eye-movement to the same location drove neurons in LIP much more than neurons in PRR. This finding contrasts the former idea that PPC contains a general saliency map, which combines all bottom-up and top-down activity for certain locations (as proposed by, e.g., Goldberg). The effector-specificity of the subpopulations in PPC gives some physiological hint on how tightly coupled attention and movement preparation are. As a sensorimotor interface (Buneo, Jarvis, Batista, & Andersen, 2002; Buneo & Andersen, 2006) the output of populations in PPC may simultaneously be projected in two directions. Direct feedforward connections (Matelli, Govoni, Galetti, Kutz & Luppino, 1998; Johnson, Ferraina, Bianchi & Caminiti, 1996) provide premotor and supplementary motor areas with the spatial coordinates of intended movement goals (Pesaran, Nelson, & Andersen, subm.). The same signals, however, may also be back-projected (top-down) to visual areas and there selectively guide processes of visual selection.

Frontal areas. In the frontal cortex, the frontal eye field (FEF) was found to play a crucial role not only in planning and executing saccadic eye movements but also in covert orienting of attention. Recent studies addressed the causal relationship between neural activity in this area and attentional shifts by directly manipulating neuronal signals (Moore & Fallah, 2004; Moore & Armstrong, 2003; Wardak, Ibos, Duhamel & Olivier, 2006). Perturbing the neural signals in the oculomotor circuit had a measurable effect on spatial attention and the representation of visual input.

In a study by Moore and Fallah (2004) monkeys were trained to detect the dimming of a peripheral target stimulus. The subthreshold stimulation in the retinotopic FEF that did not evoke a saccade, nonetheless improved the discrimination performance at exactly that location in space, at which a suprathreshold stimulation would have elicited a saccade (i.e. in the 'movement field' of the cell). The increase was found only when the FEF representation and the target were spatially overlapping (similar results were observed by Cavanaugh & Wurtz, 2004, in the superior colliculus). Moore & Armstrong (2003) similarly stimulated the FEF while simultaneously recording in V4. Indeed, the very brief subthreshold stimulation enhanced visual responses in V4 neurons at retinotopically corresponding locations. Converging evidence comes from an experiment by Wardak, Ibos, Duhamel & Olivier (2006). Here, the deactivation of FEF in one hemisphere not only increased the latencies of saccades in an eye movement task but also increased the search times in a feature-conjunction search task with controlled eye fixation. Although these studies favour the premotor theory of attention, showing that attention and eye movements share common networks in the brain, it is not clear whether both functions are provided by the same neurons. Rather, two populations may be intermingled and it might be hard if not impossible to selectively manipulate the one or the other. Sato & Schall (2003) recorded spikes from single units in FEF while the monkey performed an anti-saccade task. The analysis revealed two intermixed types of neurons in FEF: One type were pure motor neurons, which selected the endpoint of the anisaccade and showed no response for the peripheral cue. Another type of visuo-motor neurons, however, initially selected the peripheral cue and then changed their response to a better representation of the saccade goal on the opposite side. Only this second type of neurons mirrors the attentional shift from the cued position to the saccade goal. Thompson, Biscoe & Sato (2005) confirmed this neuronal diversity by employing a search task that did not involve any saccades to be prepared but instead a manual response. The motor-neurons did not exhibit any increased activity if the search target fell in their receptive field. However, the visually responsive neurons exhibited significantly greater activity if the search target was inside the receptive field (compared to those trials with a distractor inside the field). The selective activity in the visually responsive neurons of FEF corresponded to the spotlight of attention. The authors have interpreted these results as evidence for a functional divergence of spatial attention and eye movements within FEF.

1.5 Multiple movement goals

According to Allport 'effector systems are typically limited to carrying out just one action of a given kind at a time' (Allport, 1987, p. 396). This is the reason why selection-for-action is necessary (p. 397). Similarly, Neumann (1987) pointed out that one important function of selection mechanisms is to avoid the behavioural chaos that would result from an attempt to simultaneously perform all possible actions for which sufficient causes exist' (Neumann, 1987, p. 374). These important conceptualizations have inspired many empirical studies that focused on selection-for-action of single targets for single movements. For example Deubel, Schneider & Paprotta (1998) and Deubel & Schneider (2004) suggested a 'one-target-at-a-time' mechanism that always selects only one movement goal at a given point in time.

However, many actions that humans perform outside of laboratory settings are more complex and often involve more than one effector and/or multiple movement goals. This becomes obvious in examples of bimanually coordinated movements where the movements of both effectors are directed to different points in space (see Chapter 4). Another instance is the eye-hand coordination as documented for example in an object manipulation task by Johansson, Westling, Bäckström & Flanagan (2001). Here, the eyes and hands are sometimes simultaneously moved, but towards different locations. An important question is therefore how the attentional system selects visual information if more than one location is relevant as the movement target. Multiple goal positions may also be involved in fast movement sequences of a singular effector (see Chapter 2 and 3). In this case, several movement steps may be prepared in advance, because the inter-movement interval is arguably too short in order to allow for purely serial programming. Two types of findings support this line of arguments. First, eye-tracking studies repeatedly reported so called 'look-ahead' fixations where participants made saccades to objects that were important for the task only at a much later point in time (Mennie, Hayhoe & Sullivan, 2007; Pelz & Canosa, 2001). They addressed the question when visual information has to be gathered to guide subsequent movements. Second, several studies on the encoding of movement sequences in motor-related areas of frontal cortex (e.g., Mushiake, Saito, Sakamoto, Itoyama & Tanji, 2006; Tanji & Shima, 1994; Halsband, Matsuzaka & Tanji, 1994) demonstrated that the brain encodes multiple steps of a planned movement sequence as well as its exact timing (Fuji & Graybiel, 2003(@; Histed & Miller, 2006). Indeed, some studies on covert attention-for-action (e.g., Godijn & Theeuwes, 2003; Baldauf, Wolf & Deubel, 2006) found first evidence that in movement sequences several movement goals are selected in advance by means of covert attention.

1.6 Splitting of attention

The selection of multiple future movement goals is closely connected to the question of whether attention can be split among several locations. Up to now this question is still under debate. Several authors reported data that showed that attending to two locations in space facilitated also intermediate locations (Heinze, Luck, Munte, Gös, Mangun & Hillyard, 1994; Sagi & Julesz, 1986; Podgorny & Shepard, 1983). Hence, the attentional focus – often implicitly hypothesized as a spotlight (see Eriksen & Yeh, 1985; Eriksen & James, 1986) – was supposed to be undividable and to always facilitate vision in a uniform region of space (see also VanRullen, Carlson & Cavanagh, 2007). On the contrary, other studies reported findings supporting the view that attended zones could be separated by unattended regions (e.g., Müller et al., 2003; Müller & Hübner, 2002; Godijn & Theeuwes, 2003; Hahn & Kramer, 1998; Kramer & Hahn, 1995; LaBerge & Brown, 1989; Egly & Homa , 1984; Shaw, 1978; Shaw & Shaw, 1977; Beck & Ambler , 1973). Castiello and colleagues asked participants to attend zones of variable sizes in opposite hemifields and to react on the appearance of a stimulus. Interestingly, the authors found an inverse relationship between the reaction times and the size of the attended region, suggesting that subjects divided their attention into independent foci rather than covering both cued regions with one widened attentional spotlight (Castiello & Umilta , 1990; Castiello & Umilta, 1992(@). Egly & Homa (1984) found perceptual facilitation in a ring-shaped region without any attentional effects in the enclosed disc.

One crux of arguing for the splitting of attention is that such effects can often be alternatively explained by a moving-spotlight model. This model assumes that only a small area is attended at any point in time. In order to attend to more than one location, the focus must rapidly shift between them. Consequently, the question about the speed of attention and the dwell time during attentional fixations is of primary interest. Several studies have tried to determine how long it takes to voluntarily shift attention to an endogenously cued location (Logan, 2005; Theeuwes, Godijn & Pratt, 2004; Müller, Teder-Salejarvi & Hillyard, 1998; Ward, Duncan & Shapiro, 1997, 1996; Moore, Egeth, Berglan & Luck, 1996; Duncan, Ward & Shapiro , 1994; Madden, 1992;

Kroese & Julesz, 1989). On the basis of empirical data, Logan estimated that it takes about 70 ms to encode a spatial cue and another 90 ms to subsequently allocate attention to the cued location (Logan, 2005). Moore and colleagues used a so-called dwell-time paradigm (similar to the attentional blink paradigm), in which participants had to identify two objects that were briefly presented in close temporal proximity (i.e., with a small SOA, see Moore, Egeth, Berglan & Luck, 1996). They showed that the first object interferes for about 200 ms with the second one. Theeuwes and colleagues (Theeuwes, Godijn & Pratt, 2004) directly measured the serial deployment of attention with simultaneously presented stimuli. A central arrow cued one quadrant of the visual field and subjects had to covertly attend to this location. A second arrow at the covertly attended location pointed to the location that had to be attended next (in clockwise or counter-clockwise direction). Participants had to discriminate after each trial the letter that had been presented at this finally cued location. All the stimuli were presented simultaneously. In order to test when attention is where in the periphery, a small square was flashed at various SOAs requiring an immediate, speeded manual response (probe reaction time task). The results of this experiment showed an attentional dwell time of about 250 ms, as well. The obtained estimates suggest that attentional facilitation at several positions occurring within a short time window (less than 150 ms or so) can not be explained by high-speed serial shift models (see also, e.g., Duncan, Ward & Shapiro , 1994). In all of the following three studies (Chapter 2-4) the question of parallelism is tackled by extra experiments.

2 Properties of attentional selection during the preparation of sequential saccades

ABSTRACT

We examined the allocation of attention during the preparation of sequences of saccades in a dual task paradigm. As a primary task, participants performed a sequence of two or three saccades to targets arranged on a circular array. The secondary task was a two-alternative discrimination in which a critical discrimination stimulus (digital ’E’ or ’Ǝ’) was presented among distractors either at one of the saccade goals or at any other position. The findings show that discrimination performance is enhanced at all the saccade target locations of the planned sequence, while it is close to chance level at the positions that are not relevant for the saccade sequence. An analysis of the discrimination performance at the intermediate locations indicates that saccade target selection involves spatially distinct, non-contiguous foci of attention. Further, our findings demonstrate that the movement-relevant locations are selected in parallel rather than serially in time. We conclude that during the preparation of a saccade sequence – well before the actual execution of the eye movement - attention is allocated in parallel to each of the individual movement targets.

2.1 Introduction

Several empirical studies on saccadic eye movement preparation demonstrated that visual attention shifts in advance of movement initialization to the location, to which an eye movement is planned (e.g., Hoffman & Subramaniam, 1995; Kowler et al., 1995; Deubel & Schneider, 1996; Schneider & Deubel, 2002). The attention mechanism, which provides the relevant spatial information about the target ('selection-for-action' Allport, 1987), was assumed to be identical to the mechanism that filters visual input in purely perceptual tasks (coupling of 'selection-for-action' and 'selection-for-perception'). These studies investigated the deployment of visual attention before single eye movements to a target position and found preferential processing at the intended target location. Similar findings were drawn for goal-directed hand movements such as reaching and grasping, indicating that the coupling of visual attention and action preparation is not limited to the eye movement system, but is probably a general mechanism independent of the effector system used (Deubel, Schneider & Paprotta, 1998; Castiello, 1996; Schiegg, Deubel & Schneider, 2003; Deubel & Schneider, 2004; Craighero, Fadiga, Rizzolatti & Umilta, 1998; Bonfiglioni & Castiello, 1998; Kritikos, Bennett, Dunai & Castiello, 2000).

In everyday life, however, movements are often complex and not always restricted to single targets. In natural behaviour, many actions are rather action chains consisting of several components. These individual parts have to be linked together in a movement program in order to be performed fluently. Hayhoe, Land & Shrivastava (1999) for example studied action sequences in everyday tasks like sandwich making, and analyzed how the action-relevant visual information is gathered during the planning and the execution of the actions (see also Land, Mennie & Rusted, 1999). As an important finding, it turned out that under free viewing conditions, the observers systematically foveated objects that were crucial for the planning of the future action components. But action sequences do not only play an important role when humans manipulate objects. Also in the context of eye movement control, sequential aspects of movement preparation may be important. Under normal viewing conditions humans make about three saccades per second. So, while inspecting a visual scene, humans redirect their gaze about every 300 ms in order to foveate new locations and to extract further information. In demanding visual search tasks, for example, complex scan paths can be observed. In order to better understand how information about the searched items is gathered it is essential to know how such saccade sequences are planned. Since these saccades often occur in a very rapid order, it is likely that longer parts of the eye movement pathway may be planned in advance. The question arises whether and how the planning of a sequence of several saccades is also reflected in the way attention is deployed before the eye movements. One possibility is that attention may spread over the whole saccade path even before the first eye movement starts. In this case information about all target stimuli would be available already before any eye movement is initialized. The processing of visual-spatial information that is relevant for the second or third eye movement of the sequence may then take place already before the onset of the initial saccade, in order to build a complete movement plan in advance of the action.

An alternative hypothesis is that in actions composed of several sequential movements the selective processing of the relevant information is also purely sequential, such that processing of the second target would occur only after the first movement is completed. Following this model, just the actual target of the next saccade may be selected, and visual attention may be linked only to the impending goal. Saccade sequences would then be programmed in a step-by-step manner.

To date few studies have directly investigated the selective information processing before sequential movements. We (Baldauf, Wolf & Deubel, 2006) recently examined the allocation of attention during the preparation of sequences of manual pointing movements in a dual task paradigm. In an experimental approach very similar to the one used in the present study, the participants had to perform a sequence of two or three reaching movements to targets arranged on a clock face. The secondary task was a discrimination task in which a perceptual discrimination target was presented among distractors either at one of the movement goals or at any other position. The findings clearly revealed that discrimination performance was superior at the locations of all movement targets while it was close to chance at the positions that were not relevant for the movement. Moreover, the results suggested that all movement-relevant locations were selected in parallel rather than serially in time, and that selection involved spatially distinct, non-contiguous foci of visual attention. We concluded that during movement preparation – well before the actual execution of the hand movement - attention is allocated in parallel to each of the individual movement targets.

The question that arises is whether similar properties can be found also for the programming of sequences of saccadic eye movements. Indeed, two studies (Gersch et al., 2004; Godijn & Theeuwes, 2003) recently investigated the dynamic deployment of attention during the preparation of saccade sequences, however, with basically different results. Gersch et al. studied attention during intersaccadic pauses in an experiment that used self-paced, repetitive saccade sequences along circularly arranged target boxes but not cues. As a secondary task, their subjects were asked to discriminate the orientation of Gabor stimuli that were briefly presented at one of these target boxes while sequences were in progress. The authors found facilitation of discrimination performance only at the actual fixation position and at the target location of the impending saccade, but no enhanced processing of the next target position. They concluded that attention during sequences of saccades is only deployed to the impending goal position, but that further targets of the eye movement sequence are not attended. Godijn & Theeuwes (2003) studied attention before the sequence began when subjects were concerned with the initial preparation of responses and interpretation of cues. The participants had to perform speeded double saccade sequences. In their dual task paradigm, the perceptual task was to identify letters that were presented tachistoscopically near the first and second saccade goal just before initialisation of the sequence. Quite in contrast to the findings of Gersch et al., the results revealed that identification performance was facilitated close to the landing position of both the first and the second saccade in the sequence. This suggested that before the initialisation of such double saccade sequences both goal positions are attended in parallel.

One important purpose of the present research was to further elucidate the question of whether attentional deployment before saccade sequences is limited to the goal of the first saccade, or rather spreads to further targets of the planned sequence. In addition, there were three further major questions that we addressed in our study.

First, given that attention indeed spreads further along the saccade path before the initiation of a saccade sequence (Godijn & Theeuwes, 2003), the question arises whether this selection of multiple goal positions implies that attention is then split into distinct, non-contiguous foci as suggested for hand movement sequences (Baldauf, Wolf & Deubel, 2006). From the previous studies it remains unclear whether the measured facilitation effects are restricted to the saccade goals. Alternatively, the selective facilitation at both saccade goal positions may be the result of a widening of the attentional focus such as to cover both movement goals. The fact that Godijn & Theeuwes (2003) found enhanced discrimination performance at positions close to the actual saccade goals would be compatible with this alternative conjecture.

A second question addressed here was whether the selection of multiple saccade goals is temporally bound to the point in time that directly precedes the start of the saccade sequence. How is attention distributed at movement initiation if the goal positions are cued well in advance of movement onset? A spatial precue may allow selecting the goal positions in advance, and attention may then no longer be necessarily deployed to the saccade targets when the movement sequence is started. In accordance with this hypothesis, Deubel & Schneider (2003) showed that participants were able to withdraw attention from the target of a pointing movement (but not of a saccade) when the target was cued long before the onset of the movement. We test in an additional experiment whether subjects selectively attend to the target positions before the movement starts even though they had sufficient time to prepare for the saccade sequence in advance. This may indicate that in order to make a saccade sequence attention remains focused on the goal locations just until the movements are initialized.

Finally, a third central research question was related to the preparation of even longer saccade sequences. Do still more complex, triple step sequences of saccades also imply the selection of all target positions as it was shown for triple hand movement sequences in reaching tasks (Baldauf, Wolf & Deubel, 2006)? Alternatively, the selection of saccade target positions might be restricted to only two positions. In the present study the allocation of attention prior to the execution of sequences of saccades was examined in a dual-task paradigm. Participants were asked to perform a two-alternative letter discrimination task while preparing sequential saccades to several targets. In a first experiment (Experiment 1.1a), participants were required to execute a sequence of two eye movements to targets on a circular array of characters, arranged like a clock face. While the goal of the initial movement was cued by a central arrow, the second movement goal was then to move to the item two clockwise positions from the previous. We asked whether the preparation of this sequential saccade task would involve superior perceptual performance at both movement-relevant locations, as compared to the movement-irrelevant locations. Also, we were interested in the question of whether a possible facilitation at both the first and the second movement target position is due to a widening of the attentional spotlight over both target positions, or rather due to a division of attention among spatially non-contiguous, distinct attentional locations. Therefore, we also determined discrimination performance at the intermediate location between both movement goals. In Experiment 1.1b we presented a spatial precue that indicated the saccade target positions, long before an auditory tone provided the ’go’-signal for the saccade sequence. We studied in this experiment whether attention would still be focussed on both the first and the second saccade goal, when the movement targets were cued well in advance, while the saccade sequence was elicited by a later acoustical ’go’-signal. Experiment 1.2 asked whether multiple targets are selected before movement onset in even longer eye movement sequences involving three targets. Finally, Experiment 1.3 used a matching paradigm to study whether multiple movement targets are selected serially or in parallel.

2.2 Experiment 1.1

2.2.1 Methods

Participants. Eight students (aged between 24 and 27 years, five female) were paid for their participation in experiments 1.1a and b. They had normal or corrected-to-normal vision. All participants were right handed and had right eye dominance. The study was carried out along the principles of the Helsinki Declaration and with the understanding and written consent of each participant.

Apparatus. The participant sat in a dimly illuminated room. The stimuli were presented on a 21-inch colour monitor with a frame frequency of 100 Hz, at a spatial resolution of 1024 x 768 pixels. The active screen size was 40 x 30 cm; viewing distance was 80 cm. The visual stimuli were presented on a grey background, which was adjusted to a mean luminance of 2.2 cd/m^2. The moderate background brightness is important to minimise the effects of phosphor persistence (Wolf & Deubel, 1997). The luminance of the visual stimuli was 23 cd/m^2.

The movements of the right eye were recorded using a Dual-Purkinje-Eyetracker with a spatial resolution of 0.1 degree of visual angle; the eye position signal was sampled at a frequency of 400 Hz. Head movements were restricted by an adjustable rest for the chin and the forehead

Procedure – Experiment 1.1a. The sequence of stimuli in a typical trial of Experiment 1.1a is shown in Figure 2.1a. At the beginning of each trial, a display appeared, which contained a central fixation cross and a circular arrangement of twelve premask characters (each of which resembled a digital ’8’), that were positioned on an imaginary circle with a radius of 5.0 degrees around the central fixation. The horizontal width of the premask characters was 0.6 deg of visual angle; their height was 0.95 deg. The participants were asked to initially fixate the cross at the screen centre. After a random delay of 700 -900 ms, the central fixation cross was replaced by a small arrow that indicated one of the surrounding characters as the first saccade target (1st ST). Simultaneously with this movement cue an acoustical beep was presented. The participants were required, upon the onset of the movement cue, to make a sequence of two eye movements, with the first saccade aimed at the cued target. After the completion of the first saccade, the second saccade had to be directed to the character located two clock positions further in the clockwise direction (Second saccade target, 2nd ST). Participants were instructed to perform this eye movement sequence as quickly and precisely as possible.

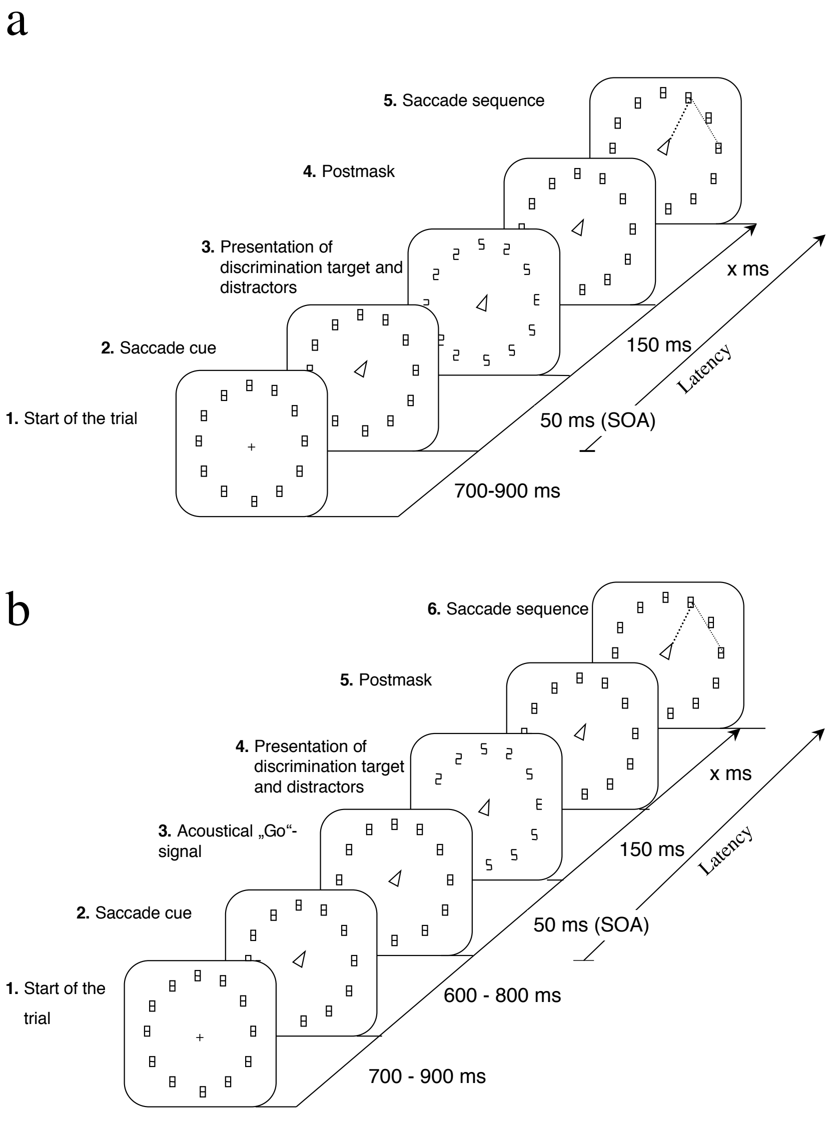


Abb. 2.1: **(a)** Stimulus sequence in Experiment 1.1a. After a random delay the central fixation cross was replaced by a small arrow that indicated the first saccade goal. Upon the onset of this saccade cue, the participants had to perform a double saccade sequence, with the first saccade aimed at the cued target the second saccade directed to the character located two positions further in the clockwise direction. With a SOA of 50ms the premask characters changed into a critical discrimination target DT (resembling digital ’E’ or ’Ǝ’) and distractors (digital ’2’ or ’5’). After a presentation time of 150 ms, all symbols were post-masked. At the end of each trial, the participants indicated by button press which of both discrimination targets had been presented. **(b)** Sequence of stimuli in Experiment 1.1b. After appearance of a spatial cue indicating the target of the initial saccade, the initialisation of the eye movement sequence had to be withheld until an acoustical go-signal was presented.

With a stimulus onset asynchrony (SOA) of 50 ms after the appearance of the central movement cue, 11 of the 12 premask characters changed into distractors (resembling digital ′2′or ′5′), while one premask changed into the critical discrimination target (DT) which resembled either the character ′E′ or ′Ǝ′. After a presentation time of this critical display of 150 ms, the discrimination target and the distractors changed back to the initial mask symbols. At the end of each trial, the participants indicated, by pressing one of two buttons, which of both discrimination targets had been presented. This non-speeded response was given on a keypad with the left hand.

Procedure - Experiment 1.1b. Stimuli and procedure were similar to Experiment 1.1a except that the cue now indicated the first saccade goal well in advance of the movement, while the subject was instructed to delay the saccade until a tone provided the go-signal for the eye movement sequence. The tone had a frequency of 400 Hz and was presented with a variable delay of 600 to 800 ms with respect to the spatial precue. Again, the participants were instructed to perform a double sequence of saccades, as fast and as accurately as possible, to the indicated position and then to the mask element two positions further in clockwise direction. Figure 2.1b provides a sketch of the temporal sequence of the stimulus presentation in this experiment.

Design. Initially, each participant performed a training block consisting of 84 trials which were not included in the data analysis. After initial training, the participants performed four experimental blocks, each consisting of 84 trials. Only six out of the twelve mask positions (at 1, 3, 5, 7, 9 and 11 o′clock) were possible saccade goals. Since the second eye movement had to be aimed to the item located two clock positions further from the initial target, both movement targets were separated from each other by an intermediate item. Thus, possible saccade sequences were directed to 1 and 3 o′clock, 3 and 5 o′clock, 5 and 7 o′clock, 7 and 9 o′clock, 9 and 11 o′clock, or 11 and 1 o′clock. The critical factor that was varied in this experiment was the position where the discrimination target was presented, relative to the instructed movement targets (factor DT position). This factor had four levels: (1) The discrimination target was presented at the first movement target (condition ′1st ST′), (2) DT was shown at the second movement target position (condition ′2nd ST′), (3) DT appeared at the location between both movement targets (condition ′between′), and (4) DT appeared at any of the remaining positions that were movement-irrelevant in that they were neither targets of the movement sequence nor located between the movement-relevant locations (condition ′other′).

The discrimination target appeared with equal probability at any of the six possible movement goals or at the position between both saccade goals, such that the movement cue had no predictive validity as to the likely location of where DT would be presented. In half of the trials, the discrimination target was the character ′E′, in the other half a ′Ǝ′ was shown. In total, this led to 84 different conditions (6 ST positions x 7 relative DT positions x 2 types of DT). The conditions were selected at random in each trial. Data analysis and rejection of trials. The eye movements were recorded on a PC during sessions and evaluated off-line by custom software. In order to determine latencies and amplitudes of the saccades, an off-line program first searched the eye movement traces for the first point above (or below) the vectorial velocity threshold of 15 deg / sec. The beginning and the end of the saccades were then calculated as linear regressions in a 20 ms time window around these threshold points.

In order to ensure that the discrimination target was no longer present when the eye movement started, trials with onset latencies of the initial movement below 200 (equivalent to 50 ms SOA, plus 150 ms DT presentation time) were excluded from further analysis. We also discarded trials where movement onset latency was above 500 ms. Finally, trials in which the first saccade target was missed by more than 2 deg or the movement erroneously was executed toward a non-cued target position were classified as sequence errors and were not analyzed further The accuracy of the perceptual performance can be expressed by the percentage of correct decisions on the identity of the discrimination target; since there were two response alternatives, chance level was at 50%. Statistical analyses in this and the following experiments included repeated-measure analyses of variance. Post-hoc comparisons were done with t-tests. All p-values were Bonferroni-corrected or, in case of pairwise t-tests, Holm-corrected. Statistical analyses were performed with the 'R' statistical package (Ihaka & Gentleman, 1996).

2.2.2 Results

Discarded trials. In Experiment 1.1a 13.3% of all trials had to be discarded because of too short movement latencies. Only 3.8% of trials had to be discarded because the saccadic response was too late. In another 6.7% of the trials saccade sequence errors occurred, these trials were also excluded from further analysis. In Experiment 1.1b 17% of all trials had to be discarded because of too short latencies and 4% because the saccadic response was too late. In 11% of trials one of the saccade goals was missed.

Movement performance. After the initial training blocks, all participants produced saccades with consistent accuracy and latency. Figure 2.2 shows the endpoints of the first (black) and the second (red) saccades for all eight participants (data from Experiment 1.1a). It can be seen that the eye movement sequences were performed quite accurately. The mean spatial distance between the instructed first target and the landing position of the initial saccade was .67 deg (SE = 0.15 deg). In Experiment 1.1b, mean spatial error was .69 deg (SE= 0.19 deg) and .71 deg (SE = 0.24 deg).

Mean latency of the initial saccade with respect to cue onset was 281 ms (SE=25.6 ms) in Experiment 1.1a. The second movement of the sequence was executed with an average latency of 552 ms (SE= 43.6 ms) after the presentation of the movement cue.

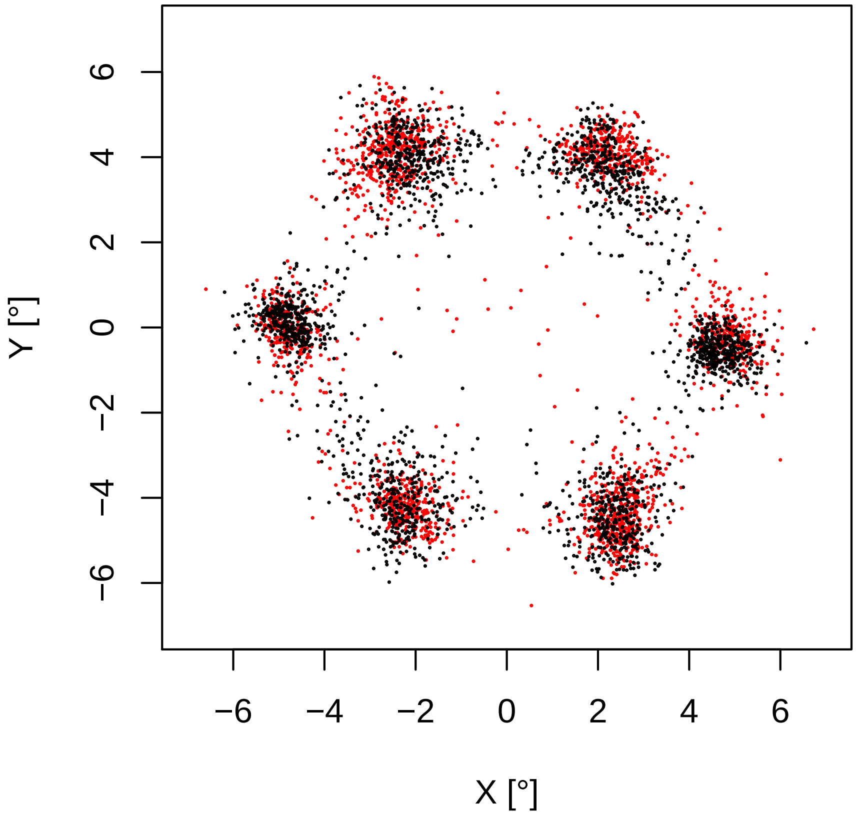


Figure 2.2: Final horizontal and vertical eye positions after the first (black) and the second (red) saccade of the double saccade sequences.

ANOVA showed no significant effect of the factor DT position on the latency of the initial saccade of the movement sequence, F(3,21) = .1.278, p> .30. This is important for the interpretation of the results, since it makes sure that the presentation of the critical discrimination stimulus ('E' vs.'Ǝ') does not affect the motor programming, for example such that motor responses would be delayed for the cases where the discrimination target (DT) does not coincide with a movement goal. In Experiment 1.1b similar movement parameters were observed. Here, the initial saccade started with a mean latency of 324 ms (SE =10.17 ms) after presentation of the (auditory) go-signal. The second saccade had a mean latency of 597 ms (SE= 39.0 ms), measured from auditory cue presentation.

Perceptual performance. The accuracy with which participants identified the discrimination target served as our measure of the spatial allocation of attention before the onset of the eye movement sequence. The black bars shown in Figure 2.3 represent discrimination performance as a function of the position of DT relative to the saccade target positions in Experiment 1.1a. As can be seen, discrimination performance was close to chance level at the movement-irrelevant locations (condition 'other'), with a performance level of 54% (SE= 3.7%) correct. On the other hand, perceptual discrimination was best at the location of the first saccade target (condition '1st ST'), yielding 90.2% (SE = 3.1%) correct. Discrimination performance at the goal of the second saccade (condition '2nd ST') deteriorated to 70% (SE = 4.9%), which is still well above chance. Thus, at both the first and the second saccade goal, the planning of the eye movement causes clear and significant benefits for perceptual processing, as compared to the movement-irrelevant locations. Of particular interest was the discrimination performance at the intermediate position, between both saccade goals (condition 'between'). The data clearly show that performance drops to chance at this intermediate location, yielding a discrimination performance of only 56.9% (SE =

2.8%) correct.

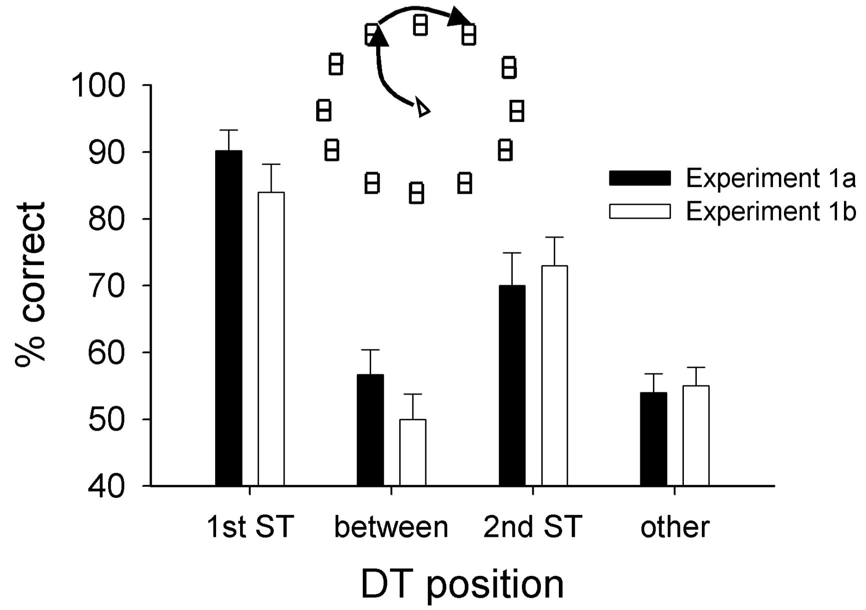


Figure 2.3: Discrimination performance in Experiment 1.1a (filled bars) and Experiment 1.1b (open bars). The proportion of correct responses in the discrimination task is shown as a function of the location of the discrimination target relative to the saccade goal positions. The bars represent averages across all participants; the error bars show one standard error. Chance level is at 50% correct.

These findings were confirmed by further statistical analyses. Pairwise post-hoc comparisons showed that performance at the first saccade target was significantly better than at the movement-irrelevant locations, t(7)= 6.789, p<.001. Also, discrimination performance at the second saccade target position differed significantly from performance at the movement-irrelevant locations t(7)= 2.916, p< .001 and from the performance at the first saccade target, t(7)= 3.873, p< .001. Furthermore, perceptual discrimination at the location between both movement targets (condition 'between') differed significantly from both the performance at the first saccade target (t(7)= 6.248, p <.001), and at the second saccade target (t(7)= 2.375, p <. .049), but it did not differ from the performance at the movement-irrelevant positions, t(7)= .541, p> .5.

The open bars in Figure 2.3 represent discrimination performance as a function of the relative DT position, averaged across the nine participants in Experiment 1.1b. Although the precue provided spatial information about the target locations well in advance of the movement onset, the pattern of discrimination performance is quite similar to that in Experiment 1.1a. A one-way ANOVA was computed for the factor DT position. The analysis yielded a significant main effect of relative DT position, F(3, 21)=38.45, p< .001. As in the first experiment, discrimination was superior when the discrimination target was presented at the first movement position, yielding 84% (SE = 4.2%) correct responses. Performance decreased at the second sequential saccade goal to 73% (SE =4.3%) correct discriminations, respectively. Performance was close to chance level at the remaining, movement-irrelevant positions (55%, SE=2.8%) as well as at the intermediate position between both saccade targets (50%, SE=3.8%). A post-hoc comparison showed a significant difference between discrimination performance at the first and the second saccade target, t(7)= 3.11, p > .010. Further, perceptual performance levels at both the first and second movement goal were significantly better than performance at the remaining, movement-irrelevant positions (t(7)= 6.59, p< .001. and t(7)= 3.48, p> .01). The performance at the position between both saccade goals was significantly different from performance at 1st ST, t(7)=-7.25, p< .01, and at 2nd ST, t(7) = 4.14, p< .01, but did not differ from the value at the remaining positions, t(7)= .661, p> .51.

2.2.3 Discussion

The results of Experiment 1.1a show that in double saccade sequences, both movement goals are selected even before onset of the initial movement, in a spatially distinct way. The discrimination performance is best at the first saccade target position and slightly lower at the goal of the second saccade in the sequence. Clearly, objects that are not relevant to the programming of the required eye movement sequence are not selected. It can be concluded that before movement onset, attentional selection is spatially highly specific to the saccade goals. This is in line with previous findings of Kowler et al. (1995) and Deubel & Schneider (1996), who demonstrated a narrow, spatially specific attentional selection of the goal of a single saccadic eye movement, before saccade onset. Interestingly, discrimination performance is also close to chance level at the item located intermediate to both saccade goals, i.e., at the item that is located on the movement trajectory of the second eye movement. This striking finding demonstrates that the improved performance at the first and second eye movement goal does not result from a widening of the attentional focus (Eriksen & Yeh, 1985). Rather, it is consistent with the assumption that attentional selection can involve spatially non-contiguous locations. In Experiment 1.1b a spatial precue was presented that indicated the saccade target positions, before an auditory tone provided the 'go'-signal for the saccade sequence. If the distribution of visual attention to all movement goals is crucial for the initialization of the movement plan, the pattern of facilitation should not differ significantly from the pattern observed in Experiment 1.1a without such a pre-cue. Alternatively, the selection of the sequential target positions may be temporally independent of the initialisation of the sequence, and may be completed before movement onset. Then, a precue specifying the saccade targets well in advance to the required eye movement may be sufficient to pre-select the relevant positions and to store the target locations in a short-term memory buffer. This would possibly allow the system to disengage attention from the target positions before the onset of the movement sequence - attention could then be distributed over the visual field according to other task demands. Since the participant in our secondary task was instructed to report a discrimination target that was presented at either of several possible positions, the most efficient strategy would then be to distribute visual resources equally over all positions in the visual field.

The results of Experiment 1.1b however show that even when the target positions are specified well in advance of the movement, visual attention is still restricted to the saccade goals at the moment when the participant has to initialize the eye movement sequence. So, although there is ample time to prepare the movement plan in advance, this does not allow the participants to distribute their attentional resources during the movement preparation to other positions than the saccade. This finding is compatible with the assumption that there is an obligatory coupling between attention and saccade preparation.

2.3 Experiment 1.2

Experiment 1.1 demonstrated that for a sequential eye movement aimed at two targets, attention spreads to the second target even before the onset of the first saccade. The question arises whether such a perceptual performance advantage at the movement-relevant locations can be also observed at further saccade goals in even longer sequences. Therefore, we extended the eye movement sequence required in the oculomotor task by another saccade, which resulted in requiring the participants to perform a triple sequence of saccades along the mask items on the circular display. The focus of analysis was on the question of whether even three saccade goals would be attended before the onset of the movement sequence.

2.3.1 Methods

The eight participants in this experiment were the same as in Experiment 1.1. The same stimuli were used. The procedure was also similar to the previous experiment

(Exp.1.1a) except that the participants were now required, after having performed an eye movement to the first (cued) and then to the second movement target, to add a third saccade, directed to the location two clock positions ahead, in a clockwise direction (an illustration of this movement sequence is given in the inset of Figure 2.4). The factor DT position had the following four levels: (1) The discrimination target was presented at the first saccade target (condition ′1st ST′), (2) DT was shown at the second saccade target position (condition ′2nd ST′), (3) DT was shown at the third saccade target position (condition ′3rd ST′), and (4) DT appeared at any of the remaining letter positions that were movement-irrelevant in that they were not targets of the eye movement sequence (condition ′other′). Again, the discrimination target appeared with equal probability at any of the six possible saccade goals (1 o′clock, 3 o′clock, 5 o′clock, 7 o′clock, 9 o′clock or 11 o′clock). In half of the trials, the discrimination target was the character ′E′, in the other half a ′Ǝ′ was shown. In total, this led to 72 different conditions (6 cued ST positions x 6 relative DT positions x 2 types of DT). The conditions were selected at random in each trial. To become familiar with the new requirements, participants initially performed a training block. Then, participants performed four experimental blocks with 72 trials each.

2.3.2 Results

Discarded trials. 9.6% of all trials in this experiment had to be discarded because of too short or too long movement latencies. Another 4.2% of trials were classified as sequence errors and were also excluded from further analysis.

Movement performance. Although the required movement sequence now involved three consecutive saccades, landing positions were still close to the instructed saccade targets. The mean spatial distance between the final landing position of the sequence and the centre of the instructed saccade target was 0.61 deg (SE = 0.14 deg). Average latency of the initial movement of the sequence was 286 ms (SE = 9.05 ms) with respect to the presentation of the saccade cue. The second saccade followed with a mean latency of 505 ms (SE= 16.7 ms), and the third and final saccade occurred with a mean latency of 660 ms (SE= 24.1ms), measured from the point in time when the cue was presented. Saccade latencies were again analysed as a function of the position of the discrimination target relative to the eye movement targets. The statistical analysis of the eye movement data revealed that also in this experiment, the latencies of the sequential saccades were independent of the position of the discrimination target. Separate analyses of variance showed no significant main effect of factor DT position on the latencies of the first, second and third saccade, F(3, 21) = 1.669, $p > .20$, F(3, 21) = 2.45, $p > .09$, and F(3, 21) = 0.07, $p > .97$, respectively. It can be concluded that the oculomotor task was not specifically affected by where, relative to the saccade target locations, the discrimination stimulus was presented. By this analysis we made sure that the presentation of the critical discrimination stimulus ('E' vs.'Ǝ') does not affect the motor programming, for example such that motor responses would be delayed for the cases where the discrimination target (DT) does not coincide with a movement goal. Perceptual performance. Figure 2.4 displays perceptual performance at the various relative DT locations. As in the previous experiments, it can be seen that perceptual performance was best when DT was presented at the goal of the initial saccade in the sequence, resulting in 87.4% (SE = 1.73%) correct decisions. Perceptual performance dropped to 74% (SE = 4.3%) at the position of the second saccade target. Remarkably, the performance level of 87.4% at the first and 74% at the second saccade target position are very similar to the corresponding performance values of the Experiment 1.1a and b, indicating that the requirement to plan a third movement did not hamper discrimination performance at the initial movement location. Finally, and most interestingly for the purpose of this experiment, perceptual performance was still significantly above chance even at the third movement location, yielding 71% correct (SE = 3.8%). In contrast, performance at the remaining, movement-irrelevant positions was close to chance level (55%, SE = 4.5%).

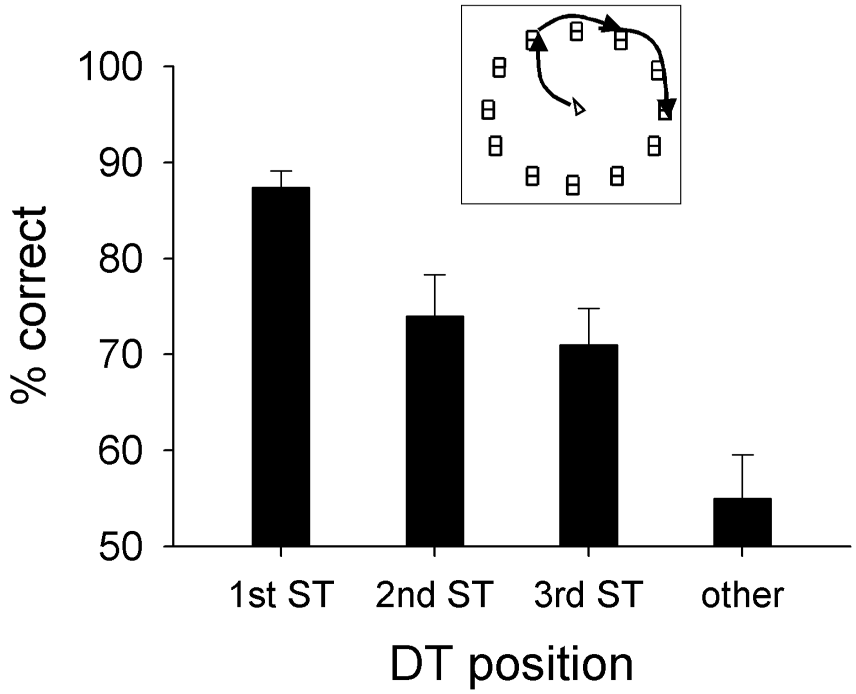


Figure 2.4: Experiment 1.2. Discrimination performance in the discrimination task as a function of the relative location of the discrimination target. The bars represent averages across all participants. The error bars show one standard error.

Statistical analysis confirmed a significant effect of the factor DT Position on discrimination performance, F(3, 21) = 22.53, $p < .001$. Pairwise t-tests showed that the difference in performance at the first and the second saccade goal was significant, t(7)= 2.543, $p < .034$, as well as the difference between the performance values at the first and the third saccade goal, t(7)= 3.14, $p < .016$. Discrimination performance at the second and the third position did not differ significantly, t(7)= .599, $p > .55$. Importantly, however, discrimination performance at the first, second and third saccade targets each differed significantly from the average performance at the movement-irrelevant locations (t(7)= 6.02, $p < .001$, t(7)= 3.478, $p < .002$, and t(7), $p < .023$, respectively).

2.3.3 Discussion

The results of this experiment show that when eye movement sequences consisting of even three consecutive saccades are prepared, all three movement-relevant goals are perceptually selected before the initial eye movement starts. This finding implies that during the period of eye movement preparation, attention is deployed, in a highly selective manner, to all three saccade goals. The data also indicate that the discrimination performance at the first and the second saccade goals is not markedly deteriorated in comparison to the results of Experiment 1.1. This means that the requirement to consider three instead of two sequential saccade goals does not entail that attentional resources are withdrawn from the first and the second target position.

2.4 Experiment 1.3

The previous experiments demonstrated that, during the preparation and before the onset of a sequence of saccades, all eye movement goals are attended, resulting in a discrimination performance at each of these positions that is superior to the performance at the movement-irrelevant locations. The important question arises whether the attentional deployment in this situation occurs in parallel, or serially in time. In order to investigate this question further, we studied perceptual performance at two spatially separate positions simultaneously in a same-different matching task. This task can only be solved if participants manage to attend to both stimulus locations simultaneously. In order to ensure that participants would not be able to shift their attention between the discrimination targets while they were displayed on the screen, the presentation time of the critical discrimination stimuli was reduced to 60 ms (for a similar approach see Godijn & Theeuwes, 2003).

2.4.1 Methods

Participants. Seven participants (four female, aged between 24 and 28 years) were tested in this final experiment. Five of them had already participated in the previous experiments.

Procedure. The stimulus array and the timing of the stimulus sequence were modified as shown in Figure 2.5. At the beginning of each trial, a display consisting of a fixation cross and four mask elements was shown. The mask elements appeared on the diagonals at an eccentricity of 5 deg from the central fixation. We decided to use fewer mask elements than in the previous experiments in order to diminish the effects of lateral masking and thus to facilitate the perceptual task (see Bouma, 1970, 1973; Intriligator & Cavanagh, 2001). This allowed to considerably reduce the presentation time of the critical display that contained the discrimination target, as compared to the previous experiments. 1500 ms after the presentation of the premask characters, an arrow appeared at the central fixation that pointed to one of the mask elements. Upon the onset of this movement cue, participants performed a double saccade sequence, with the gaze being directed to the indicated mask element first and then to the element at the next position, in a clockwise direction. With a SOA of 50 ms after the presentation of this movement cue, two of the mask elements changed into the critical discrimination targets, which resembled digital ’E’ or ’3’, while distractor stimuli (digital ’2’or ’5’) were shown at the other two locations of the array. This display was presented for only 60 ms, then discrimination targets and distractors were replaced by the mask elements. After performing the saccade sequence, participants indicated whether the two discrimination targets that had appeared during the preparation period of the eye movement sequence had been the same or different.

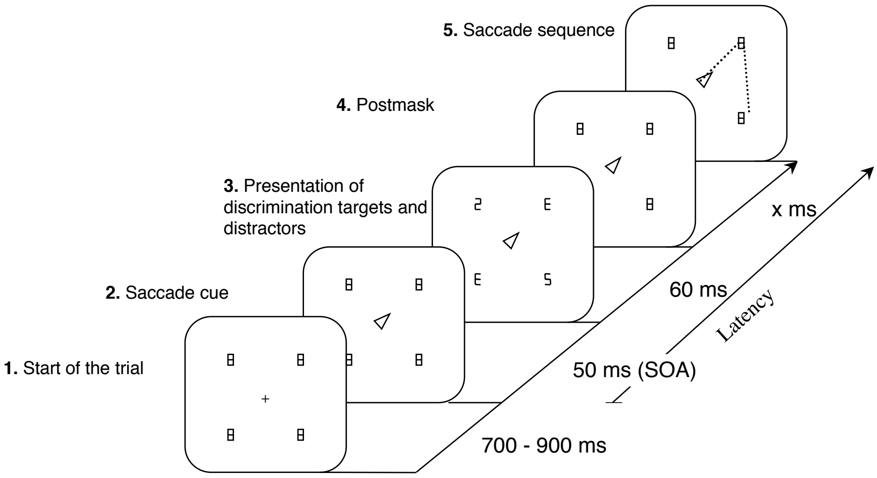


Figure 2.5: Stimulus sequence in Experiment 1.3. The secondary task required a same/different decision on the identity of the two discrimination targets that were presented for 60 ms.

Design. To become familiar with the task, participants initially performed a training session consisting of 96 trials. Then, each participant performed four experimental blocks consisting of 96 trials each. The central arrow cued one of the four target positions, selected at random. Given the four target locations, there resulted six different combinations of where the two discrimination targets could appear on the display. The discrimination targets 'E' and '∃' were presented with equal probability. In half of the trials the discrimination targets were identical, in the other half of the trials they were different. Altogether, this led to 96 different conditions (4 ST positions x 6 possible DT arrangements x 2 types of DT x 2 types of DT equality). These conditions were presented in randomised order. The central movement cue had no predictive validity for the location where the discrimination targets would be presented.

In the data analysis, we distinguished three experimental conditions, dependent on the position of the discrimination targets relative to the movement targets. In the first condition (condition 'Both'), one discrimination target was presented at the goal of the first saccade, the other discrimination target appeared at the second goal of the sequential eye movement. In the second condition (condition 'One'), only one of the locations where the discrimination targets were presented coincided with either the first or the second saccade goal, while the second discrimination target was shown at one of the movement-irrelevant locations. Finally, the third condition (condition 'None') included all those trials where both critical discrimination stimuli were presented at locations that were irrelevant for the eye movements.

2.4.2 Results

Discarded trials. Since the presentation time of the discrimination targets was only 60 ms in this experiment we excluded all those trials in which initial saccade latency was below 110 ms (50ms SOA + 60ms presentation time), or where saccade latency was more than 500 ms. Only 0.4% of the trials had to be excluded from further analysis because of too short or too long latencies. In another 7.7% of trials the first or second target was missed by more than 2 deg and therefore also discarded from further analysis. Movement performance. The analysis of the saccade landing positions again revealed a high movement accuracy, with the first saccade landing on average 0.69 deg (SE = .06deg), and the second on average 0.82 deg (SE = .08 deg) away from the centre of the instructed target item. Average latency of the initial eye movement was 231 ms (SE=6.8 ms), the latency of the second saccade was 477 ms (SE= 16.1 ms), both latencies measured from movement cue onset. Again, the latencies of the initial and the second movement were found to be independent of the relative position of the discrimination targets, F(2,12) = 0.289, p> .75, F(2, 12) = .285, p> .75, respectively.

Discrimination performance. Figure 2.6 shows discrimination performance as a function of the positions of the two discrimination targets relative to the saccade goals. Obviously, the required matching task could be solved only when both discrimination targets appeared at the movement-relevant locations (condition 'both'). In this condition, the performance was 69% (SE = 4.0%) correct. However, when only one or none of the discrimination targets were presented at movement-relevant positions (conditions 'One' and 'None'), performance levels were close to chance at 53% (SE = 2.7%) and 49% (SE = 2.5%), respectively, indicating that the required comparison between both stimuli was not possible.

A one-way ANOVA revealed a significant main effect of the relative position of the discrimination targets on the performance of the matching task, F(2,12) = 14.8, p < .001. Pair-wise comparisons showed a significant difference between the perceptual performance when discrimination targets and eye movement targets coincided, and the cases when one or when none of the discrimination targets was presented at a movement goal, t(6)= 3.44, p< .01, and t(6)= 4.47, p< .01, respectively.

2.4.3 Discussion

The results of this experiment provide strong evidence that the selection of the saccade goals, which occurs during the preparation of the sequential eye movement, can be better described as a parallel allocation of visual attention to both movement targets, rather than as a serial shift of attention between the targets.

The logic of the same-different matching task requires that the presentation time for the critical discrimination stimuli is sufficiently short to prevent the participants from shifting attention serially from one discrimination target to the next. In the present

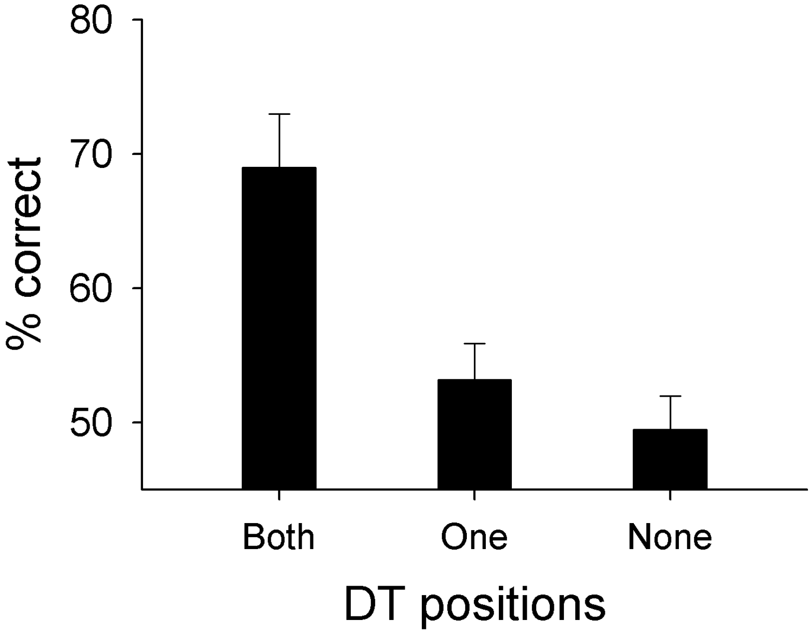


Figure 2.6: Performance in the same/different matching task of Experiment 1.3 as a function of the locations of the two discrimination targets, relative to the saccade goals. Either the locations of both discrimination targets coincided with the saccade goal positions ('Both'), or only one discrimination target was presented at a movement goal ('One'), or none of the discrimination targets appeared at a location relevant for the planned saccade sequence ('None'). The bars represent averages across all participants, the error bars show one standard error.

approach, the two discrimination targets were present on the screen for 60 ms only. In line with Kramer & Hahn (1995), Hahn & Kramer (1998), and Godijn & Theeuwes (2003) we believe that this time interval is too short to allow for a series of two endogenous attention shifts. So, there is considerable evidence that it takes 150 to 200 ms to identify a stimulus that was indicated by a precue and then to reallocate attention covertly to another position (Eriksen & Yeh, 1985; Kroese & Julesz, 1989; Madden, 1992). Ward, Duncan & Shapiro (1996) even estimated that up to 500 ms may be needed to shift attention endogenously. In a recent study Logan (2005) disentangled the time that is needed to encode a spatial cue and the attention-switching time. The author suggested that for a single target position the cue encoding takes about 70 ms and the attention switching to the cued location an additional 90 ms. Evidence for considerably faster attention shifts, so-called ′express′ attentional shifts (see e.g., Mackeben & Nakayama, 1993), are limited to peripheral cueing and to specific experimental settings, such as those involving a gap paradigm (see, e.g., Bekkering, Pratt & Abrams, 1996; Fischer & Weber, 1993).

The performance in the condition ′Both′ of the matching task can in principle be predicted from the probabilities to correctly identify the discrimination performance at the first and the second movement target. Let the probability to correctly identify the discrimination target at the first goal of the movement sequence be p_1, and the probability to identify the discrimination target at the second movement target be p_2. Consider further that a correct decision in the matching task can result either from the correct identification of both DTs, or from the incorrect identification of both DTs. Hence, the probability for a correct decision is $p_1 * p_2 + (1 - p_1) * (1 - p_2)$. Unfortunately, we did not determine perceptual performance in a single-target discrimination task for the stimulus arrangement and the presentation times of Experiment 1.3. However, assuming that perceptual performance at the first and second movement target were similar to those found in Experiment 1.1 (0.86 and 0.75, at the first and second movement target, respectively), the predicted probability for a correct decision in a matching task is 0.68 (= 0.84 * 0.73 + 0.16 * 0.27). This is very close to the value of 0.69 actually found in the matching task of Experiment 1.3, for the condition where both discrimination targets were presented at the movement-relevant locations.

2.5 General Discussion

2.5.1 Preparation of saccade sequences involves selective processing of the movement-relevant targets

Former results from both saccade and reaching tasks suggested an obligatory coupling between (dorsal) selection for action and (ventral) selection for perception (e.g., Kowler et al., 1995; Hoffman & Subramaniam, 1995; Deubel & Schneider, 1996; Deubel, Schneider & Paprotta, 1998). The aim of the present study was to extend these findings to a more complex eye movement task, namely, to saccade sequences involving two or three predetermined target locations. So, in contrast to the earlier investigations where one single object served as the movement target, the tasks presented here involved a more complex computation of motor parameters which includes several movement-relevant locations. As the central finding of the present study, perceptual performance is found to be significantly better at the locations of all movement-relevant targets, as compared to the other, movement-irrelevant locations. This suggests that before the onset of the initial saccade the second and even the third target position are selected and processed with higher priority than the task-irrelevant locations. This finding rules out a serial model of attentional deployment in which, first, the initial saccade is being prepared and executed in isolation, and only after its completion, the next part of the sequence is prepared, and so on. Quite surprisingly, the selective perceptual processing of the movement-relevant locations is even present in a task which requires a quite complex, triple sequence of saccadic eye movements (Experiment 1.2). The results are evidence that some information about subsequent saccade goals is integrated in the initial movement plan. The selection filter predefines the path of the saccade sequence segregating the visual scene into movement-relevant and movement-irrelevant locations. The deployment of visual attention emphasizes the contrast between the saccadic goals and nearby locations. This helps diminishing interference with non-target locations and facilitates the programming of precise saccade sequences. In this context it might be interesting that the order of the goals within the saccade sequence is reflected by a gradient of attentional weights. Less attention was deployed to the more subsequent goals than to the first, immediate one. Information about the order, in which the individual saccades have to be made, may be encoded in this pattern of attentional weights and could be provided to hierarchically subsequent motor areas.

The findings confirm and extent former evidence reported by Godijn & Theeuwes (2003), who studied attentional deployment in a double saccade task. Godijn and Theeuwes demonstrated that prior to the execution of a sequence of two saccadic eye movements, attention is allocated to a region in space that covers both saccade goals. As in the present study, they also found that most attentional resources are mainly allocated to locations that are close to the target of the initial movement, yielding best perceptual performance, while less processing capacity is dedicated to locations nearby the second movement goal. The present findings now specify in more detail the spatial aspect of the attentional deployment by measuring attention exactly at the saccade goals. Further, our data provide novel information about the distribution of attention among positions that are located right in-between both saccade goals.

Thus, our results present converging evidence for the assumption that attention can indeed spread along the planned sequence, and multiple target locations are selected in advance of movement initialisation. As demonstrated by our findings, this is also true for at least three goal positions in even longer eye movement sequences.

In contrast to the findings of Godijn & Theeuwes (2003) and our results, Gersch et al. (2004) found no evidence for an attentional allocation beyond the next saccade target while participants performed self-paced sequences of saccades on a circular array of items. They suggested that in sequential saccades attentional resources are dedicated primarily to the goal of the next saccade, leaving little attention for processing objects at other locations. The reasons for the discrepancies between these studies still remain unclear. One difference between the experiment of Gersch et al. and our study is that our participants were specifically instructed to perform the sequence as quickly as possible. It may be speculated that only when very fast, predetermined sequences are required, these movements are preplanned in advance of movement onset, while a slower, self-timed movement pace would allow for a sequential target processing. Additional experimental work is needed in order to answer this question. Another One important difference between Gersch et al.'s experimental task and the task in our study is that Gersch et al. measured attention during repetitive sequences without any cue-interpretation component. In our task the central cue had to be encoded, interpreted and converted to a representation of the motor sequence. Finally, in the present study, as well as in the work by Godijn & Theeuwes, attention was measured during the interval before the onset of the sequence, while Gersch et al. measured attention during the ongoing sequence. This could possibly account for the discrepancy because different events occur during initial preparation of a motor sequence than during the performance of the sequence itself (see a broader discussion of this point in Gersch et al., 2004). Additionally the results of Experiment 1.1b show that all saccade targets are selectively attended just before the eye movement sequence starts, in spite of the fact that the subjects had the opportunity to prepare the saccade sequence well in advance of the go-signal. This may indicate that the distribution of attention to the goal locations is crucial for the execution of the movement plan.

2.5.2 Evidence for the division of attention among non-contiguous locations

The analysis of perceptual performance at the item located in between the first and the second saccade target in Experiments 1.1a and b revealed that discrimination performance is at chance level if the discrimination target appeared at the item located between both saccade goals of a planned sequence. This indicates that attention was not directed to this intermediate position, while the movement targets located closely to the left and to the right were selected with high efficiency. Together with the experimental evidence discussed below that attentional allocation is parallel rather than serial in time, this result demonstrates that attention is divided among the spatially non-contiguous movement targets. The spatial selectivity of the attentional focussing is amazingly high, given the target items were only 2.6 deg apart, and appeared at 5.2 deg in the visual periphery.

This finding rules out the alternative explanation of an attentional zoom lens, which would assume a widening of the attentional focus to include both saccade target locations (e.g., Eriksen & James, 1986). Rather, the results support a model in which attention can be deployed to multiple, non-unitary regions of visual space, so that several objects can be selected individually. The finding that under certain conditions attention can be divided among non-contiguous locations is in line with results of Hahn and Kramer (1998; Kramer & Hahn, 1995). They demonstrated that observers can concurrently attend to non-contiguous locations as long as new distractor objects did not appear between the target locations. They also showed that hemifield boundaries did not constrain the participant's ability to divide their attention. This is in line with the results of our Experiment 1.3, which demonstrates that attention can be deployed to even three separate locations that are distributed in both visual hemifields. The splitting of visual attention into two or three spatially distinct foci located on the movement-relevant items is further, striking evidence for how tightly selection-for-action and selection-for-perception are coupled (Schneider, 1995).

2.5.3 Parallel allocation of attention to the movement-relevant targets

Our experiments show that when a sequence of saccades is prepared, attention shifts to all movement-relevant targets. Our last experiment (Experiment 1.3) addressed the question whether this attentional deployment occurs in parallel, or serially in time. In a same-different matching task target letters had to be compared which were presented simultaneously at various spatial positions. Since the discrimination targets were shown only briefly (60 ms), this task could only be solved given attention can be deployed to both targets simultaneously. Indeed, the data clearly showed that the comparison was only possible if both target letters were presented at the goal positions of the double saccade sequence. This is direct evidence that multiple movement target positions are selected in parallel when they become relevant for goal-directed saccades. Similar results were reported by Godijn & Theeuwes (2003) for locations nearby the sequence goals. Our results extend and specify these previous studies by the findings that (1) intermediate locations do not benefit from the selection of adjacent goal positions, and (2) that the selection in movement preparation is not restricted to only two saccade goals. Rather, attention seems to spread along even longer paths, but with attentional weights that decline from the first to the subsequent goals.

2.5.4 Neural mechanisms

The posterior parietal region (PPC) is one of the most important neural areas for target selection in visually guided movements. Spatial information is coded in parallel in various substructures of PPC for different effector systems (Snyder, Batista & Andersen, 1997, 2000; Andersen, Snyder, Bradley & Xing, 1997; Konen, Kleiser, Wittsack, Bremmer & Seitz, 2004; Rizzolatti, Riggio & Sheliga, 1994; Graziano & Gross, 1994). One of these substructures, the retinotopically organized lateral intraparietal area (LIP), is known to be involved both in the programming of saccades and in attentional selection per se (Chelazzi & Corbetta, 2000; Colby, 1998; Colby & Goldberg, 1999; Rizzolatti, Riggio & Sheliga, 1994). Interestingly, LIP is not only connected to the frontal eye fields (FEF) and the superior colliculus (both important for computing motor commands for saccades), but also to the extrastriate visual area V4, and it seems to be an important interface between sensory processing and action preparation (Corbetta, Miezin, Shulman, & Peterson, 1991). Hahn & Kramer (1998) assumed that LIP may indeed also be crucial for the programming of sequences of saccades (see also, LaBerge & Brown, 1989). However, Mazzoni, Bracewell, Barash & Andersen (1996) showed that in a delayed memory saccade task in which double saccade sequences had to be executed, only the first saccade goal was represented during the delay period in LIP. While this study seems to imply that the parietal regions code movement intentions only for the pending movement goal, a recent fMRI study on sequential saccades by Medendorp and colleagues (Medendorp, Goltz & Vilis, 2006) reported about increased BOLD activity before the execution of double-step saccades that was found contralateral to the first and second saccade target.

On the other hand, there is some evidence from neurophysiology for a link between saccade programming in FEF and covert visual attention (see Awh, Armstrong & Moore, 2006). Most of these studies used single-cell-recordings or microstimulation. Some authors have argued that the FEF may be crucial for orienting visual attention in general (Moore & Fallah, 2001, 2004; Cavanaugh & Wurtz, 2004; Moore & Armstrong, 2003; Wardak, Ibos, Duhamel & Olivier, 2006). So the attentional signals that facilitate perception at goal locations during the preparation of subsequent saccades (Selection-for-action) may be provided by the FEF. Unfortunately, the activation in FEF before the initialisation of saccade sequences like those studied here has not yet been investigated extensively. There are some hints, however, that movement-related areas in frontal cortex may be involved in the programming of movement sequences. So, Kettner, Marcario & Port (1996) found that different neuronal populations in the dorsal section of the premotor cortex directionally code all parts of arm movement sequences already during the delay period before of movement onset (for similar results of parallel encoding see also Mushiake, Saito, Sakamoto, Itoyama & Tanji, 2006). However, since these data also suggest that during the delay period the observed signals represent the (hand-referenced) directions of the subsequent movements, the coding would still have to be reconverted into an eye-centered frame of reference in order to provide the required attentional biases to visual areas. So, taken together, it is not clear so far which brain area(s) provide(s) the attentional signals that cause the observed facilitation at all subsequent goal locations of a saccade sequence. As Batista

& Andersen (2001) suggested, frontal and parietal regions may work in conjunction in order to plan sequences of movements.

Conclusion We studied the relation of attention and eye movement preparation in a task where sequential saccades had to be directed to multiple targets. Our results confirm former findings by Godijn & Theeuwes (2003) who used a similar experimental paradigm showing that during the preparation of a saccade sequence attention is deployed in parallel to each of the individual movement goals. Beyond this our findings demonstrate that this parallel selection of saccade-relevant locations involves spatially distinct, non-contiguous foci of visual attention. We also show that during saccade sequence preparation, at least three spatially separate targets can be attended, even if they are presented in different hemifields. Discrimination performance is always best at the first saccade position and deteriorates at further movement goals. In general, these properties are very similar to the features of attentional deployment before sequences of pointing movements, as recently studied by Baldauf, Wolf & Deubel (2006). This supports the idea that the underlying selection mechanisms are very similar - if not identical - for the different effector systems. Overall, the results are consistent with the view that eye movement preparation and selective attention are intimately related.

3 Attentional selection of multiple goal positions before rapid reaching sequences

ABSTRACT

A dot probe paradigm was used to provide physiological evidence for the parallel selection of multiple movement goals before rapid hand movement sequences. Participants executed a sequence of manual pointing movements to two out of three possible goal positions. During movement preparation a task-irrelevant visual transient (a dot probe) was flashed either at one of both movement goals, or at the third, movement-irrelevant location. The results revealed that the N1-component induced by the presentation of the dot was enhanced if the dot was flashed at one of the movement goals, indicating that both target positions were attended before the initialisation of the movement sequence. A second experiment showed that movement-irrelevant locations between the movement goals were not attended suggesting that attention splits into spatially distinct foci.

3.1 Introduction

Visual attention plays a crucial role in the selection of objects that are relevant for goal-directed actions. Also on a neuronal basis, the processes of covertly deploying spatial attention and movement preparation seem to share common circuits (e.g., Awh, Armstrong & Moore, 2006). According to the 'premotor theory of visual attention' (Rizzolatti, Riggio & Sheliga, 1994) , spatially selective attention in general is a consequence of activation in cortical areas that code space for the programming of goal-directed motor actions in so-called 'spatial pragmatic maps'. As proposed by a number of authors, different spatial pragmatic maps in parietal regions are activated depending on the type of action that is to be performed, and depending on the effector system that is to be used for these actions (e.g., Andersen, Snyder, Bradley & Xing, 1997; Andersen & Buneo, 2002; Colby, 1998; Snyder, Batista & Andersen, 2000; Kawashima, Naitoh, Matsumura, Itoh, Ono & Satoh, 1996; Jeannerod, 1994).

At a behavioural level, a variety of studies have shown that the intention to perform a certain movement causes a covert shift of visual attention to the goal location in advance to the movement initialisation (for an overview see Chapter1, sections 1.3-1.3).

Often, however, motor behaviour is more complex and, under natural conditions, many actions are movement chains consisting of several components. In natural sequential tasks (e.g., Pelz & Canosa, 2001; Hayhoe, Shrivastava, Mruczek & Pelz, 2003) it has been demonstrated that human actors are planning their movements several steps ahead and often gather important visual information about future reaching goals in advance of execution by so called 'look-ahead' fixations. Mennie and colleagues (Mennie, Hayhoe & Sullivan, 2007) studied eye-, hand-, and head- movements while subjects built models with wooden slats. The authors found that anticipatory look-aheads occurred before about 20% of all reaching movements and improved subsequent visuo-motor coordination. In order to perform fluently in a sequential movement task it may be efficient to take subsequent movements into account for the execution of the impending movement. The question arises whether in such complex actions, composed of several sequential movements, the selective processing of relevant visual information is also sequential, such that processing of the second target would occur only after the first movement is completed. Ballard and colleagues (Ballard, Hayhoe & Pelz, 1995) called this a 'just-in-time' strategy. Alternatively, in fast movement sequences, the amount of time that elapses between the first and the second movement may be too short to effectively process the second subsequent goal. Some of the information processing that is relevant for the second movement part could take place already before the onset of the initial movement segment, simultaneously with the selection of the first goal. It may even be possible that all the single movement parts are assembled into one action plan for the entire sequence in advance. This would imply that all action-relevant targets are selectively processed in advance of movement onset in order to specify the necessary movement parameters (such as movement direction and amplitude, or grip orientation).

Only very few studies have investigated the specific properties of attention deployment before sequential movements. For planning of manual actions, we (Baldauf, Wolf & Deubel, 2006) studied attentional deployment in rapid reaching sequences. As a primary task participants had to perform fast double- or triple-pointing movements to various peripheral goal positions. Briefly after a Go-signal for the movement but before movement onset small target letters were presented either at one of the movement goals or at other, movement-irrelevant positions. After completion of the movement sequence, the non-speeded secondary task was to identify the target letter that had been presented during the movement preparation period. This secondary task served as a measure of the allocation of visual attention during sequence preparation. The results showed that the ability to identify target letters in the secondary task was superior at all goal locations of the planned sequence. From these findings we concluded that in rapid reaching sequences up to three target positions are selected in advance during the movement preparation interval before the first movement starts. Moreover, the analysis of intermediate locations that lay between the first and second goal of a double reach showed that attention splits into spatially distinct foci, which are selected in parallel.

The purpose of the present ERP study was to provide convergent, electrophysiological evidence that multiple goal positions are attentionally selected when sequential hand movements are planned. In the present study the allocation of attention prior to the execution of sequences of manual reaches was examined with a dot-probe paradigm. Mangun & Hillyard (1988) were the first to introduce the dot-probe paradigm to study the effects of spatially selective visual attention. Essentially, this approach uses the amplitude of the neural response elicited by a probe stimulus as an indicator of how much processing resources were allocated to that location (see also Mangun & Hillyard, 1990, 1991). The visual ERP was shown to be particularly sensitive to the direction of spatial attention. Since then, probe stimuli were used in various tasks demonstrating that dot probes presented at attended locations elicit larger sensory-evoked ERP components than stimuli at unattended locations. This was interpreted as attention modulating sensory processing in visual cortex (Mangun, Hillyard & Luck, 1993). Such attention-related modulations of sensory processing are first evident in the P1 component (Eason, 1981; Mangun & Hillyard, 1987, 1988, 1990), which arises from lateral extrastriate visual cortex (Mangun, Hillyard & Luck, 1993). However, some studies suggest that the P1 effect primarily reflects a suppression of processing at unattended locations rather than a facilitation of processing at attended locations (Luck, Hillyard, Mouloua, Woldorff, Clark & Hawkins, 1994; Luck & Hillyard, 1995). In contrast, the attentional modulation of the subsequent N1-component is assumed to reflect the enhanced visual processing of the visual stimulation at the attended location (Mangun & Hillyard, 1987, 1988, 1990).

In our paradigm these modulation effects were used to study where in the visual field attention is deployed during the preparation of sequential hand movements. Upon appearance of a cue, participants were required to execute a sequence of two pointing movements to two out of three possible locations. During the latency period between cue onset and the commencement of the movement a task-irrelevant dot probe was flashed for 70 ms. We asked whether the preparation of this sequential movement would involve enhanced visual processing at both movement-relevant locations, as compared to the movement-irrelevant location. This should result in increased N1-amplitudes evoked by the visual transient whenever the dot probe was flashed at either goal position. In contrast, the ERP component evoked by dot probes that were flashed at a movement-irrelevant location should not show any attentional modulation.

A second experiment aimed at the question of whether a possible facilitation at both movement goals results from a division of attention among spatially non-contiguous locations. Dot probes were also flashed at locations intervening the first and second reach goal. If the selection of multiple movement goals causes the focus of attention to be split into separate foci, probe stimuli that are presented at such intermediate positions should elicit N1-components with amplitudes similar to those components that were evoked by visual stimuli at task-irrelevant locations.

3.2 Experiment 2.1

3.2.1 Methods

Participants. Nine students of the Ludwig-Maximilians-University, aged between 23 and 28 years (four male), participated in the experiment. All had normal or corrected-to-normal vision and were right-handed. They were paid 9 Euros per hour for their participation and gave their informed consent in advance of the experiment.

Experimental setup. Figure 3.1 shows a sketch of the experimental setup. The participant sat in a dimly lit room. The stimuli were presented on a 21-inch colour monitor (Conrac 7550 C21) with a frame frequency of 100 Hz, providing a spatial resolution of 1024 x 768 pixels. The active screen size was 40 x 30 cm; viewing distance was 58 cm. Pointing movements were executed on a slightly inclined plane in front of the participant. A one-way mirror was adjusted in front of the subject such that the visual stimuli appeared to be projected onto the pointing plane. The mirror between the pointing plane and the participant's face avoided the occlusion of the visual stimuli by the hand or arm and also allowed hand movements without visual feedback about the position of the hand and fingers. The visual stimuli were presented on a grey background, which was adjusted to a mean luminance of 2.2 cd/m^2. The relatively moderate background brightness is important to minimise the effects of phosphor persistence (Wolf & Deubel, 1997). The luminance of the visual stimuli was 23 cd/m^2.

Pointing movements were recorded with a Fastrak electromagnetic position and orientation measuring system (Polhemus Inc., 1993), consisting of a sender unit and a small receiver mounted on the tip of the index finger of the participant's right hand. The sender unit was fixed at a distance of 60 cm from the participant. The device had a spatial accuracy of 0.8 mm. The frequency bandwidth of the system is 120 Hz,

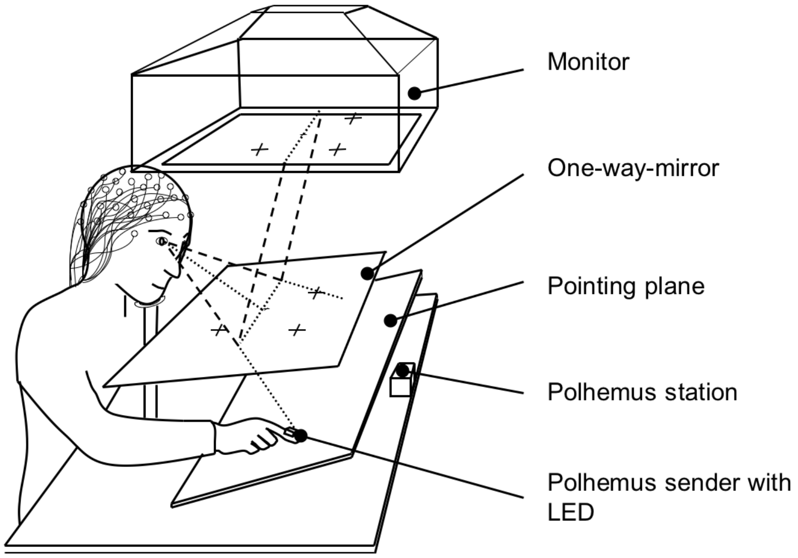


Figure 3.1: Experimental set-up. The visual stimuli were generated on a video display and projected via a half-translucent mirror onto a pointing plane in front of the participant. They appeared at a viewing distance of 58 cm. Movements of the right index finger of the pointing hand were recorded with a Polhemus Fastrak electromagnetic tracking system.

the signal delay is approximately 4 ms. In order to provide visual feedback about the spatial positions of the fingertip during an initial positioning period, a small red LED (5 mm diameter) controlled by the computer was attached to the sensor. Eye fixation was controlled by the EOG. An adjustable chin rest helped to reduce head movements. Stimuli and Procedure. Figure 3.2 shows the sequence of stimuli in a typical trial. The grey screen contained a continuously visible fixation cross at its centre. The participants were required to fixate at this central cross during the whole experimental block. At the beginning of each trial, they also positioned their right index finger at the central cross. After 400 ms a stimulus configuration was presented consisting of three crosses in three of the four corners of the screen. The crosses appeared 5 degrees in the visual periphery and extended 1.2 degrees of visual angle. After a random delay of 650-1200 ms an acoustic Go-signal was given, which had a pitch of either 200 or 500 Hz. The participants were instructed to perform a double pointing sequence to two out of the three crosses of the configuration as soon as they heard the Go-signal. If the Go-signal was a low-frequency beep, the participants first pointed to the cross in the middle of the configuration and then went on to the next cross in the clockwise direction. If they heard a high-frequency beep they first pointed to the cross in the middle and then immediately pointed to the cross in the counterclockwise direction. Participants were asked to execute the double-pointing sequence as fast and as fluently as possible. Speed and accuracy were equally stressed.

In order to determine the deployment of visual attention during the movement preparation period a task-irrelevant dot probe was flashed at a delay of 150 ms after the acoustic Go-signal – well before the initialisation of the pointing sequence – at the location of one of the peripheral crosses. The probe consisted of a circular disk with a diameter of 1.2 degree, which had the same luminance as the movement targets (23 cd/m^2). The probe was presented for 70 ms superimposed on one of the periph-

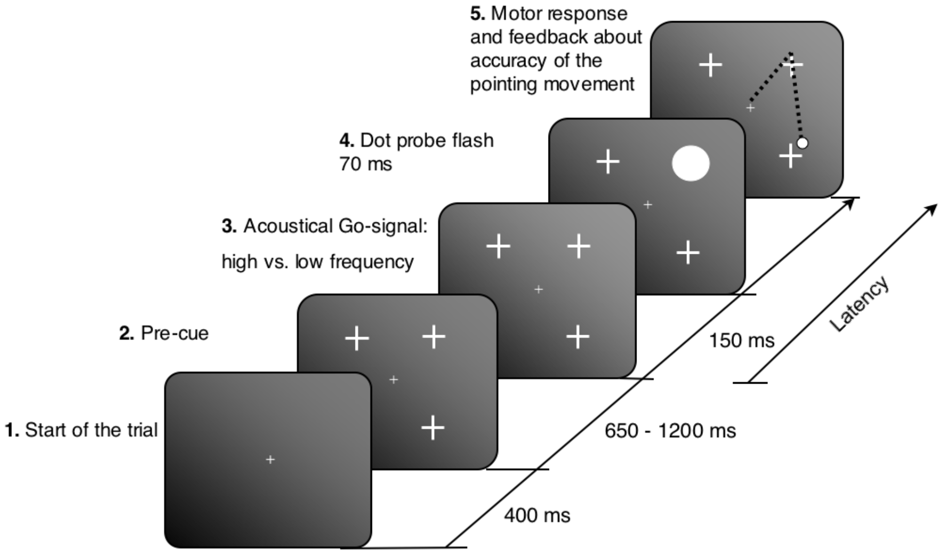


Figure 3.2: Experimental procedure in Experiment 2.1. 400 ms after the start of each trial a stimulus configuration consisting of three crosses was presented. This triangular arrangement could be oriented to any of the four quadrants. After a random delay of 650-1200 ms a high or low frequency beep was presented as an acoustical Go-signal. Upon this tone the participants were requested to perform a double pointing sequence. The first movement had to be directed to the cross at the middle position of the virtual triangle. Dependent on the pitch of the Go-signal, the second reach led to the next cross in either the clockwise (low frequency beep) or the counter-clockwise direction (high frequency beep). 150 ms after the onset of the Go-signal a dot probe was flashed for 70 ms at one of the three cross locations.

eral crosses. After the execution of the required movement sequence the participants received visual feedback about the pointing accuracy at the final goal position.

Design. Initially, each participant performed a training block consisting of 60 trials: there were not included in the data analysis. After this initial training, the participants performed five experimental blocks, each consisting of 120 trials. The critical factor that was varied in this experiment was the position where the dot probe was flashed relative to the instructed movement targets. This factor (probe position) had three levels: (1) The dot probe was flashed at the first movement target (condition '1^{st} MT'), or (2) at the second movement target position (condition '2^{nd} MT'), or (3) it appeared at the third cross of the configuration that was not a pointing goal in the present trial and therefore was movement-irrelevant ('irr'). There were four possible cross configurations corresponding to the four quadrants of the screen. The acoustical Go-signal that also coded the direction for the second part of the movement (clockwise versus counter-clockwise) was either a high- or a low-frequency beep. In total, this led to 24 different conditions (4 possible cross configurations x 2 acoustical direction cues x 3 relative probe positions). The conditions were selected at random in each trial. Each condition was repeated five times in an experimental block.

Recordings. EEG was continuously recorded by a BrainAmp system (Brain Products, Munich, Germany) from 64 Ag/AgCl electrodes mounted in an elastic cap (EasyCap, FMS). The electrodes were positioned according to the international 10-10 system and referenced to Cz. The vertical electro-oculogram (vEOG) was recorded bipolarly from electrodes above and below the left eye. The horizontal electro-oculogram (hEOG) was recorded bipolarly from the outer canthi of both eyes. Electrode impedances were kept below $5k\Omega$ and as equal as possible in all electrodes. The signals were amplified and filtered online using a 0.1-100 Hz bandpass filter; the digitalisation rate was 500 Hz. The recorded signals were then 40-Hz low-pass filtered offline.

The continuous EEG data was segmented into predefined analysis windows of 1200 ms duration, starting 200 ms prior to and ending 1000 ms after the presentation of the acoustical Go-signal. Trials with eye blinks (defined by a voltage at FPz exceeding $\pm 80\mu$V)), with saccades (a voltage at hEOG or vEOG exceeding $\pm 80\mu$V)), and with muscle artefacts (a voltage at any site exceeding $\pm 100\mu$V) were excluded from further analysis. After this rejection of artefacts there was still some residual activity in the EOG channels that was caused by small eye movements counterbalancing the deviations in head position when the reach was initialized. We corrected the ERPs for these residual eye movements by applying the algorithm of Gratton, Coles & Donchin (1983), which computes propagation factors that characterize the relationship between EOG and EEG traces.

Since the analysis of the EEG data revealed that the elicited ERPs were only very weakly lateralized, we computed separate ERP averages only for the three possible relative positions of the dot probe with respect to the actual pointing goals, irrespective of the quadrant in which the dot probe had appeared. The epochs were time-locked to the onset of the Go-signal and averages were computed relative to the 200 ms baseline before the onset of this imperative stimulus. Locking the evoked ERPs to the onset of the Go-signal seems appropriate because movement preparation and, hence, selection-for-action are hypothesized to start at this point in time. A consequence of locking the ERPs to the Go-signal is that the components elicited by the probe are shifted by the SOA between Go-signal and onset of the probe (150 ms).

The mean ERP amplitudes of the components that were elicited by dot probes appearing at the three different relative positions were analyzed in a repeated-measures ANOVA. The factors of this ANOVA were Probe position (‘1^{st} MT’, ‘2^{nd} MT’, or ’irr’) and Electrode site (with the levels ‘O1’, ‘O2’, ‘P3’, ‘P4’, ‘C3’, and ‘C4’). The analyses were based on the mean amplitude of the N1-component (relative to baseline) that was elicited by the onset of the dot probe. The statistical analyses were done with the 'R' statistical package (Ihaka & Gentleman, 1996).

3.2.2 Results

Rejection of trials due to movement error. 5.4% of all trials were discarded because the instructed target was missed by more than 3 deg. In most of these errors, participants responded incorrectly to the acoustical direction cue and executed the second movement, for example, in counter-clockwise instead of clockwise direction. 6.7% of all trials were rejected because of the occurrence of eye movements or other artefacts in the EEG (e.g.,muscle activity). Another 6.9% of trials with movement onset latencies longer than 600 ms were also excluded from further analysis. Finally, since we wanted to ensure that the dot probe was presented only during the movement preparation period, we discarded 1.5% of trials with latencies shorter than 220 ms (SOA of 150 ms plus 70 ms presentation time of the dot probe).

Movement performance. Figure 3.3a illustrates some typical trajectories for one participant. Participants performed fast and accurately in the experimental blocks. The mean pointing error between the landing positions of the first movement and the centre of the target item was 1.54 deg (SE=0.15 deg). Figure 3.3b shows the landing positions of the first (circles) and the second movement part (crosses) for all participants.

In a more detailed analysis, we calculated the directional error of the landing position at the first movement goals assigning deviations in clockwise direction with positive values and deviations in counter-clockwise direction with negative values. We tested whether the endpoints of the first movement part systematically depended on the direction of the subsequent movement. In trials with clockwise sequence production the mean directional error of the first movement component was 0.08 deg

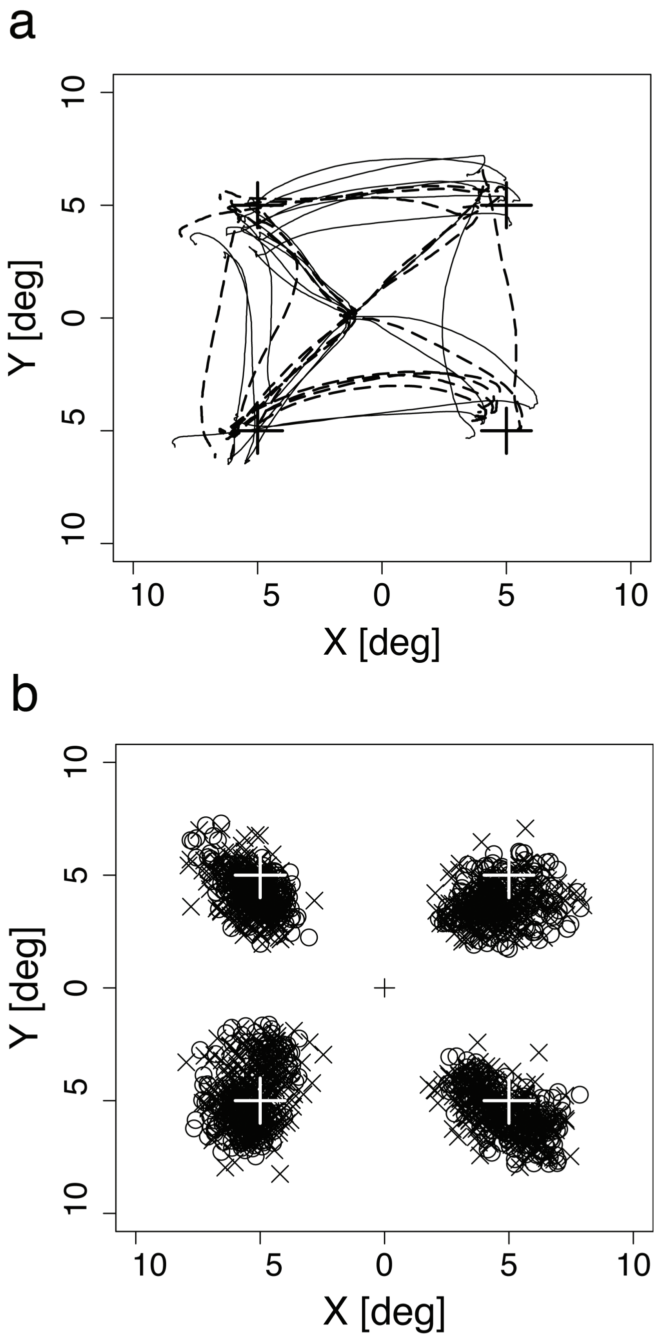


Figure 3.3: **(a)** Exemplary movement trajectories from one participant. The first movement of the double pointing sequence was directed to one of the four corners. The second movement led to the next position either in clockwise (solid lines) or counter clockwise (dashed lines) direction, depending on the acoustical Go-signal. **(b)** Landing positions of the first (circles) and second (crosses) movement of the sequence.

(SE=0.02 deg) and in counter-clockwise trials 0.10 deg (SE=0.02 deg). This difference was not significant, t(8)= 0.59 , $p > .50$, indicating that the endpoints of the first movement component did not systematically depend on whether the sequence was planned to be continued in clockwise or in counter-clockwise direction.

The initial movement started with a mean latency of 371 ms (SE = 27.4 ms) after presentation of the acoustic cue and had an average duration of 201 ms (SE= 14.7ms). The second movement of the sequence had a mean latency of 760 ms (SE= 45.7 ms), also measured from (auditory) cue onset.

Since the task-irrelevant dot probe served as a measure of the deployment of attention in the visual field, it should not affect the motor task. Specifically, it is important to ascertain that the appearance of the probe at a certain position did not hamper or delay the movement that was about to be programmed. Therefore, we analysed whether the movement latencies and / or the spatial accuracy at the first goal were dependent on the factor Probe position. For instance it may be interesting to test whether the landing positions at the first goal were slightly shifted towards the probe stimulation. An one-way ANOVA yielded no significant main effects of the factor Probe position (with the levels '1st MT', '2nd MT' or 'irr') on the latency of movement onset (F(2,16) = .711, $p > .50$). Moreover, another ANOVA did not reveal any significant effect of the 'Probe position' (with the factor levels '1st MT', 'clockwise next position' and 'counter-clockwise next position') on the directional error at the first goal, F(2,16)= 0.006, $p > .50$. Therefore, neither the latency of the sequence initialisation nor the spatial accuracy at the first goal were systematically affected by where the dot probe appeared in relation to the movement targets. This indicates that the movement task was performed without specific spatial interference from the flashed dot probes.

Event related potentials. In order to determine the distribution of visual attention during the preparation of movement sequences we analysed the event-related potentials (ERPs) that were triggered by the presentation of the dot probe shortly before sequence initialisation. The evoked ERPs were collapsed across the four quadrants in which the dot probe could be flashed and were analysed with regard to the relative position of the eliciting dot probe stimulus in relation to the movement goals (factor Probe position with the levels: '1st MT', '2nd MT', 'irr').

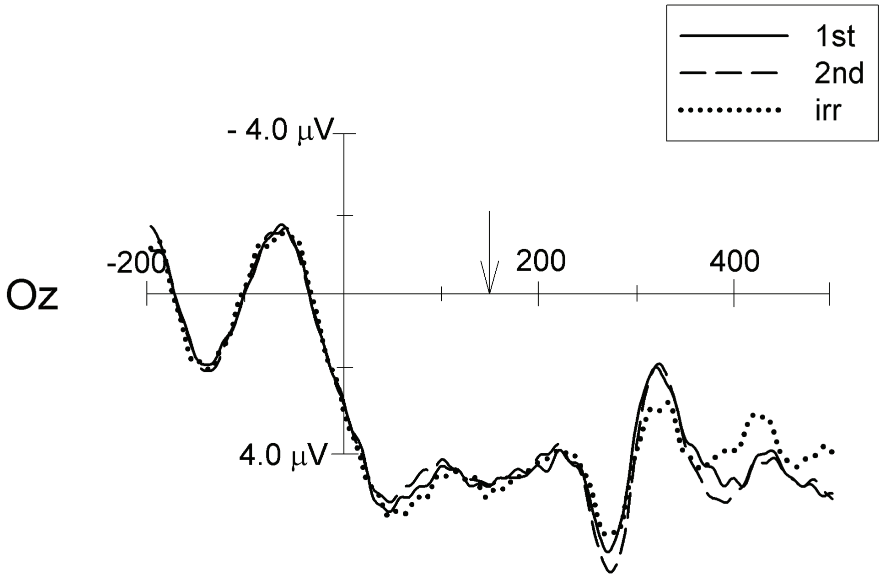


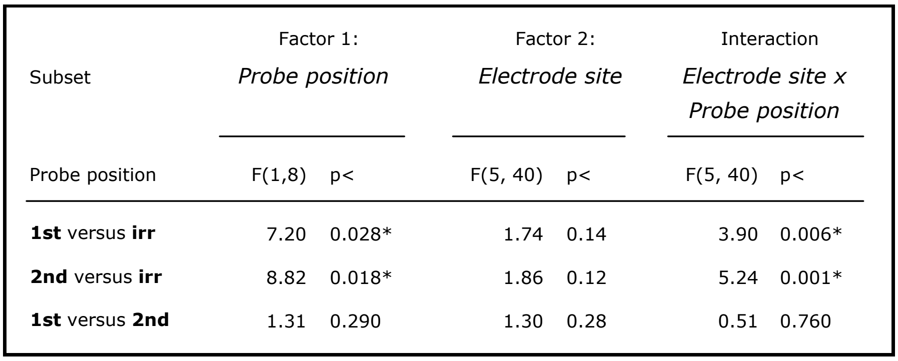
Figure 3.4: The grand-averaged ERPs evoked at an occipital site (Oz) by the presentation of dot probes. An interval ranging from 200 ms before to 500 ms after the onset of the Go-signal is shown. The dot probe could be flashed at either of three positions relative: either at the first movement target ('1st MT', solid line), or the second movement target ('2nd MT', dashed line), or at a third, movement-irrelevant position ('irr', dotted line). Waveforms are collapsed across trials with different absolute positions of the dot probe. The vertical arrow represents the onset of dot probe, which was presented with a constant SOA of 150 ms after the Go-signal.

Figure 3.4 shows the ERPs, which were evoked at the occipital electrode Oz by dot probes presented at the various relative stimulus locations. The solid line in the graph represents the ERP in response to dot probes that were flashed at the first movement goal; the dashed line shows the grand averages to dot probes presented at the second movement goal of the pointing sequence. The dotted line finally shows the ERPs to dot probes presented at the third, movement-irrelevant position of the particular trials. The ERPs were characterized by P1- and N1-components in response to the appearance of the dot probe. Since the dot probe was always presented 150 ms (SOA) after the acoustic Go-signal (the onset of the dot probe is marked by the arrow in Figure 3.4) the evoked P1 peaked at 270 ms, i.e. 120 ms after onset of the dot probe, and the N1 peaked at 320 ms, i.e. 170 ms after the dot probe appeared. The data show that the amplitude of the N1-component was enhanced if the dot probe was flashed at either the first or second goal location that were relevant for the double-pointing task. In contrast, dot probes at the movement-irrelevant position elicited smaller components. This modulation of the evoked N1-components was not affected by whether the ERPs were locked to the onset of the Go-signal or to the onset of the dot probe.

The enlargement of components evoked by dot probes at movement-relevant locations was confirmed by further statistical analyses. In order to quantitatively compare the N1-amplitudes depending on the relative dot probe positions we extracted the mean voltage in the time window 305 ms to 335 ms (peak of the N1-component at 320 ms +- 15 ms, corresponding to 170 ms +-15 ms relative to the onset of the dot probe). First, we computed a two-way ANOVA with the first factor Probe position with the levels '1st MT', '2nd MT', and 'irrelevant'. The other factor coded electrode sites and had the levels 'O1', 'O2', 'P3', 'P4', 'C3', and 'C4'. The ANOVA revealed a significant main effect of probe position on the amplitude of the N1-component ($F[2,16]= 6.76$, $p< .01$), but no significant main effect of the factor Electrode site, $F(5,40)= 1.61$, $p> .18$. Furthermore, there was a significant interaction between Probe position and

Electrode site, F(10,80)= 3.39, $p < .001$.

We conducted further analyses in order to determine which of the three relative probe positions (‘1st MT’, ‘2nd MT’, ‘irr’) differed from the other (according to, e.g., Luck, 2005). For this purpose, we ran additional two-way ANOVAs on subsets of the data that included only pairs of relative dot probe positions (i.e. ‘1st’ vs. ‘irr’, ‘2nd’ vs. ‘irr’, and ‘1st’ vs. ‘2nd’). The second factor was always ‘Electrode Site’ with the levels ‘O1’, ‘O2’, ‘P3’, ‘P4’, ‘C3’, and ’C4’. Table 4.1 provides an overview of the results of these analyses. Of special interest for the purpose of this study is that the N1-components in response to probes at the 1st as well as to those at the 2nd movement target differed significantly from the N1-components elicited by probes at movement irrelevant locations. The comparison between components in response to probes at the 1st versus 2nd movement target, however, showed no significant difference (see Table 4.1).



Subset	Factor 1: *Probe position*		Factor 2: *Electrode site*		Interaction *Electrode site x Probe position*	
Probe position	F(1,8)	p<	F(5, 40)	p<	F(5, 40)	p<
1st versus **irr**	7.20	0.028*	1.74	0.14	3.90	0.006*
2nd versus **irr**	8.82	0.018*	1.86	0.12	5.24	0.001*
1st versus **2nd**	1.31	0.290	1.30	0.28	0.51	0.760

Table 3.1: Additional ANOVAs on three subsets of the data in Experiment 2.1. Each of the subsets contains one pair of relative probe positions. The factor ‚Electrode Site’ had the levels ‘O1’, ‘O2’, ‘P3’, ‘P4’, ‘C3’, and ‘C4’ in all three subsets. The mean amplitude values are calculated for a 30 ms interval around the peak of the N1-component at 320 ms after onset of the Go-signal, i.e. 170 ms after the presentation of the dot probe.

To better establish the origin of the recorded visual activities we converted the measured voltages into reference-free current source density (CSD, see Pernier, Perrin & Bertrand, 1988) and then calculated the activation topography over the scalp, separately for each of the three conditions ‘1st Mt’, ‘2nd MT’ and ‘irr’ (Figure 3.5). To better represent the topographies in the activation maps we changed the baseline to the time interval just before the onset of the dot probe. As can be seen from Figure 3.5 the flashed probe elicited a strong event-related negativity over the occipital and parieto-occipital lobe.

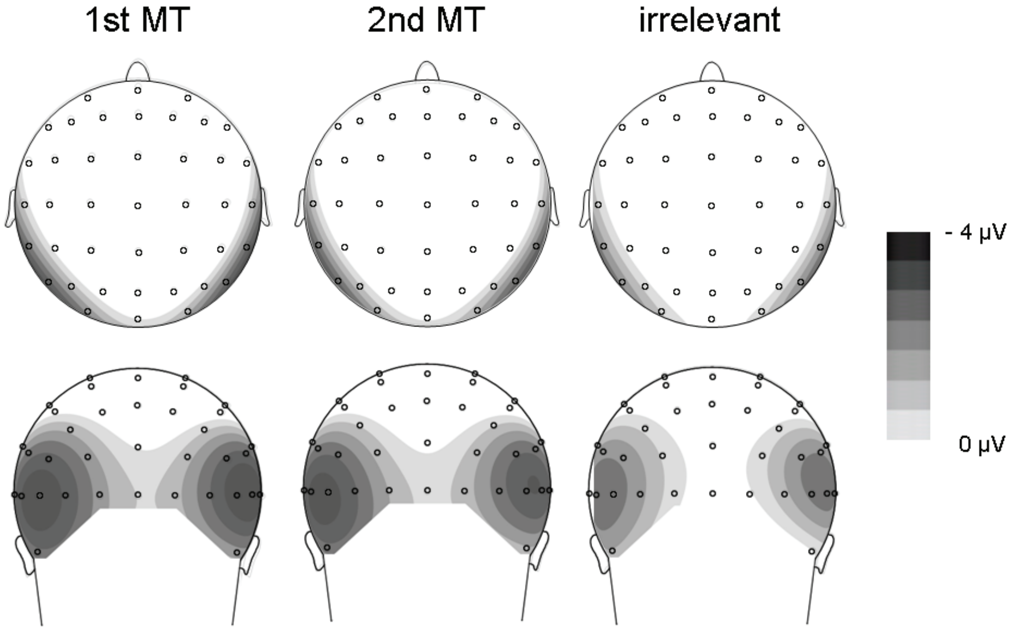


Figure 3.5: Maps of the distribution of the current source density (CSD) over the scalp. The three subplots show the activity that was evoked by probe stimuli at the 1st Mt (left panel), the 2nd MT (middle panel) or at the irrelevant position (right panel) averaged over all subjects. To better represent the topography the baseline has been change to a 200 ms interval preceding the onset of the probe stimulus.

3.3 Experiment 2.2

3.3.1 Methods

Participants, Stimuli and Procedure. Nine students, aged between 23 and 28 years (four male), participated in this second experiment. All had normal or corrected-to-normal vision and were right-handed. The same setup as in the previous experiment was used. We adjusted the configuration of the pre-cue and added intermediate non-target positions in between the potential movement goals. Figure 3.6 provides a sketch of the stimulus sequence.

The pre-cue configuration now consisted of 5 crosses that were arranged on a virtual semicircle, which was oriented towards one corner of the screen. All stimuli had the same eccentricity (5 deg) from the central fixation cross. The participants were asked to perform rapid double pointing sequences to two out of the five crosses of the configuration as soon as the Go-signal was presented. The first reach had to be directed to the central cross of the configuration. Depending on the frequency of the acoustic Go-signal (low versus high frequency beep) participants had to move on either in clockwise or in counter-clockwise direction to the next-but-one position. A task-irrelevant dot probe was flashed in each trial, 150 ms after the acoustic Go-signal. The dot probe was flashed at either the first (condition '1st MT'), or at the second movement goal (condition '2nd MT') of the particular trial or at the third - movement irrelevant – position (condition 'irr') that was at the opposite end of the configuration. Additionally, the probe could now also appear at the intervmediate position right between the first and second movement goal of that trial (condition 'inter').

Design. Each participant performed five experimental blocks. Each block consisted of 160 trials. The factor Probe Position now had the four levels '1st MT', '2nd MT', 'irr',

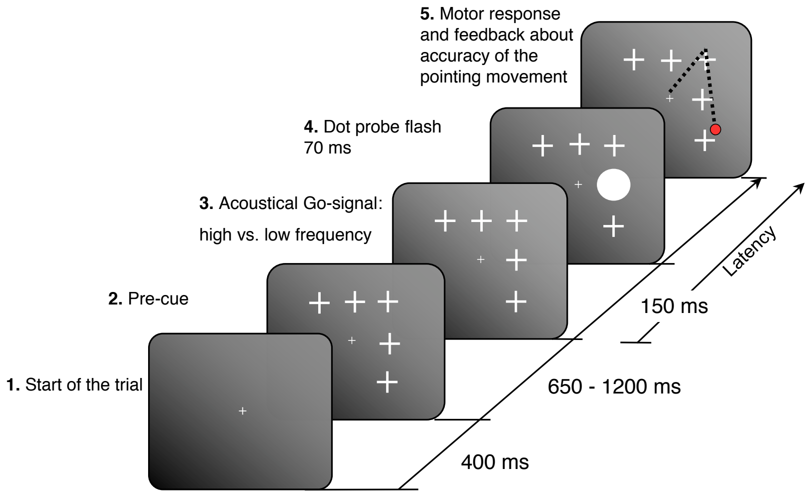


Figure 3.6: Sequence of stimuli in Experiment 2.2. After 400 ms a pre-configuration consisting of five crosses was presented that was equidistantly aligned on an virtual semicircle around the central fixation. After a random delay of 650-1200 ms an acoustical Go-signal was given in form of an high or low frequency tone. Upon this tone the participants were requested to perform a double pointing sequence. The first movement part had to be directed to the cross at the middle position of the peripheral cross configuration. The second reach lead to the cross two positions further in either clockwise (low beep) or counterclockwise direction (high beep). Shortly after the onset of the ‘Go-signal a dot probe was flashed for 70 ms at one of the cross positions.

and 'inter'. There were four possible cross configurations, corresponding to the four quadrants of the screen. There were two types of acoustical Go-signals instructing either clockwise or counter-clockwise direction for the second movement part. In total, this led to 32 different conditions (4 possible cross configurations x 2 acoustical direction cues x 4 relative dot probe positions). The conditions were selected at random in each trial.

ERP recordings. The recording parameters were the same as in Experiment 2.1. Again, the ERP responses were averaged depending on the relative position of the dot probe, irrespective of the quadrant, in which the dot probe may have appeared. The result of this procedure were separate ERP averages for the four relative positions of the dot probe in respect to the actual pointing goals. Averages were computed relative to the 200-ms baseline before the onset of the Go-signal. The statistical analysis was based on the mean amplitude of the N1-component elicited by the onset of the dot probe.

3.3.2 Results

Movement performance. 0.8% of trials had to be discarded because the movement latencies were shorter than 220 ms. Another 5.5% of the trials were rejected because the movement latency was more than 600 ms. In 4.9% the first or second movement of the sequence missed the respective target by more than 3 deg and these trials were also discarded.

The pointing movements were started after 388 ms on average (SE = 24.0 ms). The second movement of the sequence had a mean latency of 765 ms (SE= 47.3 ms), measured from auditory cue onset.

Event related potentials. The evoked potentials were averaged for each of the four possible relative positions of the dot probe. Figure 3.7 shows the ERPs evoked by the task-irrelevant visual probe stimuli at an occipital electrode site. As in Experiment 2.1, the dot probe was presented after an SOA of 150 ms after the Go-signal. We averaged the evoked ERPs locked in time to the onset of the Go-signal. As a consequence, the N1-component elicited by the dot probe is shifted in time (with the peak of the N1 component at 320 ms).

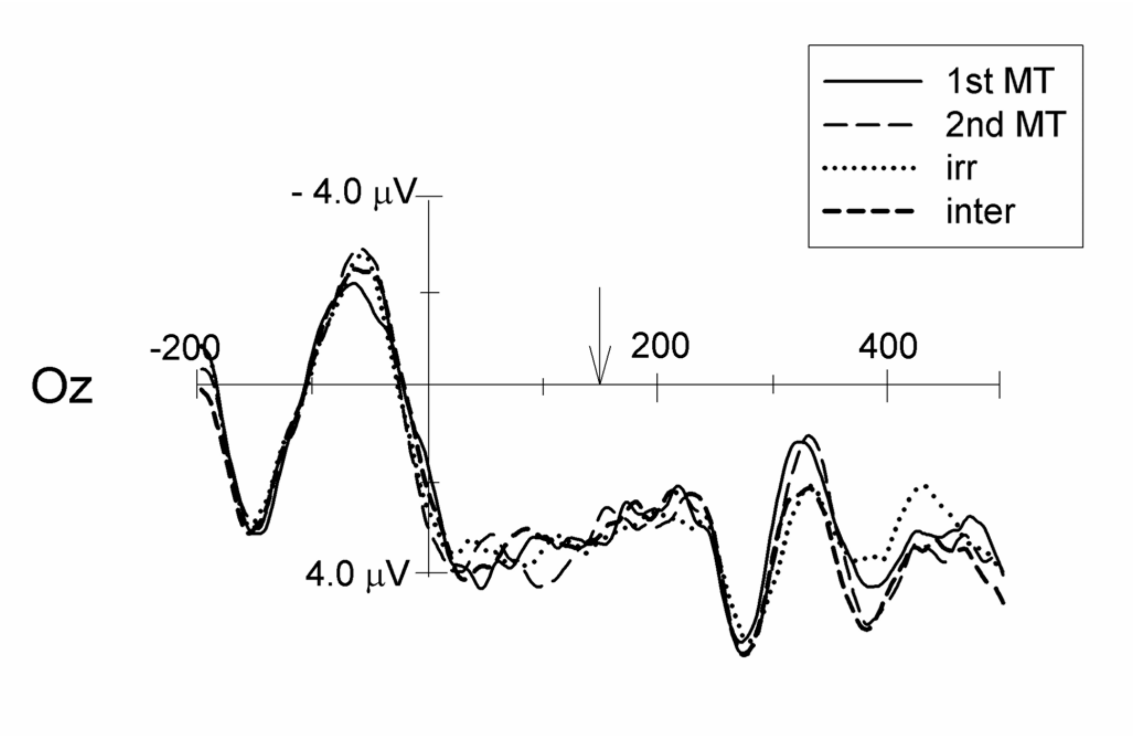


Figure 3.7: Grand-averaged ERPs at an occipital site evoked by dot probes during the preparation of a double pointing sequences. The dot probe could be flashed at either of four positions relative to the goal arrangement of the movement task: either at the first (‘1st MT’, solid line) or the second movement target (‘2nd MT’, dashed line) or at a third, movementirrelevant position (‘irr’, dotted line) or at the intermediate position between both movement goals (‘inter’, long-dashed line). Within these relative dot probe positions the waveforms are collapsed across trials with different absolute positions of the dot probe. The vertical arrow shows the onset of the 70 ms lasting dot probe flash after a constant SOA of 150 ms..

The solid line shows the ERP in response to dot probes that were flashed at the first movement goal; the long-dashed line shows the grand averages to dot probes presented at the second movement goal of the pointing sequence. The dotted line corresponds to the ERPs to dot probes at the third, movement-irrelevant position of the particular trials. The short-dashed line, finally, shows the ERP elicited by probes at the intermediate position. Most interestingly for the purpose of this second experiment, also dot probes that were flashed at the intermediate positions right between the first and second reach goal evoked only a small N1-component (short-dashed line). The results resemble the observation of Experiment 2.1 in that the amplitudes of the N1 was enhanced if the dot-probe was flashed at a location that was relevant for the double-pointing task (first and second movement goal). Importantly, dot probes at positions that were not a goal for the planned movement elicited smaller N1-components, although they were flashed at the location between both reach targets. The N1 amplitudes were compared by extracting the mean amplitude voltage in a 30 ms time window around the peak of the N1 at 170 ms (corresponding to 320 +-15 ms relative to the probe onset). A two-way ANOVA with the factors Probe Position (levels '1st MT', '2nd MT', 'irr', 'inter') and the factor Electrode Site (levels 'O1', 'O2', 'PO7', 'PO8', 'P5', 'P6', 'C5' and 'C6') revealed a significant main effect of the probe position on the amplitude of the N1-component ($F[3,24]= 5.47$, $p< .004$), but no significant main effect of the factor Electrode site, $F(7, 56)= 0.74$, $p> 0.63$. The interaction between both factors was significant with $F(21, 168)= 3.06$, $p< .005$. Additional ANOVAs were based on subsets of the data including only pairs of relative probe positions (i.e. '1st' vs. '2nd', '1st' vs. 'irr', '1st' vs. 'inter', '2nd' vs. 'irr', '2nd' vs. 'inter' and 'irr' vs. 'inter'). The second factor was always Electrode Site with the levels 'O1', 'O2', 'PO7', 'PO8', 'P5', 'P6', 'C5' and 'C6'. Table 3.2 provides an overview of the results of these analyses. As the most important outcome of this second experiment it can be seen from Table 3.2 that dot probes at the 1st or 2nd MT elicited significantly higher N1-amplitudes than probes at the intermediate, irrelevant position, F[1,8]= 5.91, p< .04 and F[1,8]= 6.38, p< .035, respectively.

Subset	Factor 1: *Probe position*		Factor 2: *Electrode site*		Interaction *Electrode site x Probe position*	
Probe position	F(1,8)	p<	F(7, 56)	p<	F(7, 56)	p<
1st versus **2nd**	0.03	0.86	0.44	0.87	2.06	0.06
1st versus **irr**	10.0	0.02*	0.85	0.55	0.94	0.48
1st versus **inter**	5.91	0.04*	0.93	0.48	2.53	0.03*
2nd versus **irr**	7.38	0.03*	0.61	0.75	1.57	0.16
2nd versus **int**	6.39	0.03*	0.64	0.72	4.53	0.01*
int versus **irr**	0.89	0.37	1.34	0.24	0.82	0.57

Table 3.2: ANOVAs on six subsets of the data in Experiment 2.2. Each of the subsets contains one pair of relative probe positions. The factor ‚Electrode Site' had the levels 'O1', 'O2', 'PO7', 'PO8', 'P5', 'P6', 'C5' and 'C6' in all six subsets. The mean amplitude values are calculated for a 30 ms interval around the peak of the N1-component at 320 ms after onset of the Go-signal.

3.4 Discussion

3.4.1 Visual selection of multiple movement goals

In this study we used a dot probe paradigm (see also, e.g., Mangun & Hillyard, 1988, 1991; Heinze, Luck, Munte, Gös, Mangun & Hillyard, 1994; Eimer, Forster, Van Velzen & Prabhu, 2005) in order to test where in the visual field attention is deployed while sequences of manual pointing movements are prepared. For this purpose a visual probe was presented briefly after a Go-signal for the movement sequence but well before the movement initialisation, at one of several positions. In each trial the transient could be presented either at the instructed first or second movement goal, or at positions that were movement-irrelevant in that particular trial. The results show that the N1-components, which were elicited at occipital and parietal sites by the dot probes, differed depending on their relative positions with respect to the motor task goals. Dot probes that were presented at the first or the second movement goal elicited N1-components with higher amplitudes compared to dot probes that appeared at movement-irrelevant locations. We interpret these enlarged components that occurred in response to probes at goal positions as enhanced visual processing and attribute this enhancement to selection-for-action by visual attention.

The dot probe paradigm has been used in several EEG-studies to determine the distribution of attention in the visual field. It is well known that N1-components evoked by dot probes similar to the one used in the present study are modulated by visual attention (e.g., Mangun & Hillyard, 1991; Mangun, 1995; Hopf & Mangun, 2000; Eimer, Forster, Van Velzen & Prabhu, 2005). The present study provides the first electrophysiological evidence for the assumption that during the preparation of pointing sequences multiple goal positions of the planned movement sequence are attended in advance to the sequence initialisation.

This is in line with our previous behavioural study on the selection of multiple goal positions during the preparation of fast hand movement sequences (Baldauf, Wolf & Deubel, 2006) , where we showed that during sequence preparation participants could better identify target letters at all goal locations of a planned sequence than at movement-irrelevant positions. We also showed that more attention is allocated to the first reach goal than to subsequent and that intermediate positions that lie between two reaching targets are not selected. During the short interval of movement programming the visual space seems to be subdivided quite flexibly into movement-relevant and movement-irrelevant parts, depending on the demands of the movement task. Interestingly, the N1-components that we recorded in the present experiments in response to dot probes flashed at the first and second movement goal did not differ from each other. This suggests that the first and the second movement goal are attended to about the same degree, which is in some contrast to our behavioural findings. One possible explanation for these differing results may be that the observed modulation of the N1-component did not result from an enhancement of those amplitudes that were evoked by probe stimuli at the movement goals, but rather resulted from a decrease of the amplitude in response to probes at movement-irrelevant locations. Following this alternative view, the Go-signal in Experiment 2.1 may indicate that one of the potential goals, namely the irrelevant location, has to be ignored and attention may not be allocated towards the movement goals but shifted away from the position that is no longer relevant for the upcoming movement.

3.4.2 Relation to other recent ERP-studies on movement preparation

Other recent EEG-studies have also investigated the relationship between covert shifts of attention and manual response preparation. Eimer and colleagues for example conducted an ERP study to explore whether shifts of somatosensory attention are triggered when unimanual responses are prepared (Eimer, Forster, Van Velzen & Prabhu, 2005). In their task subjects had to prepare to lift either their right or left index finger after a certain delay. The authors observed enhanced somatosensory ERP components when during a delay period task-irrelevant tactile probes were delivered to the cued hand. Analogue results were reported by further studies using similar approaches (e.g., Van der Lubbe, Wauschkuhn, Wascher, Niehoff, Kömpf & Verleger, 2000; Eimer, Van Velzen & Driver, 2002). These findings were interpreted as covert shifts of visual attention as a consequence of movement preparation. However, all these studies investigated manual response tasks that did not involve actual goal-directed reach movements to certain target positions but mere effector selections (e.g.,lifting the left vs. right index finger). They provide some evidence that the preparation of a motor response with either the left or right hand causes attention to be shifted to the chosen effector side. In contrast, our results show that attention-for-action shifts to target locations of visually guided reaches, similar to what has been previously observed in the programming of single saccades (see, e.g., Eimer, Van Velzen, Gherri & Press, 2006; Van der Stigchel & Theeuwes, 2005). Furthermore, most physiological studies on the preparation of reaching movements measured preparation activity during an instructed delay before the Go-signal. This may limit the extent to which these results can be generalized since in natural environments movements are only rarely performed under delay conditions. In contrast, we measured the deployment of visual attention to reach goals shortly after the Go-signal, before the reach sequence started.

3.4.3 Spatially distinct foci of attention

In our second experiment we presented the dot probe also at an irrelevant intermediate position between the first and second goal. By this we wanted to analyse whether the participants attended to an extended region of space if they are requested to perform speeded actions to multiple movement goals. The results of Experiment 2.1 could be explained by a possible widening of the atenional focus as to cover both target positions simultaneously (Eriksen & Yeh, 1985; Eriksen & James, 1986). The results of Experiment 2.2 however showed clearly that the N1-component evoked by dot probes at intervening locations was not enhanced in comparison to other movement-irrelevant positions. This suggests that the parallel selection of multiple reach goals also implies a splitting of the attentional beam into non-contiguous foci.

These results are in line with previous findings in sequential movement production (Godijn & Theeuwes, 2003; Baldauf, Wolf & Deubel, 2006; Baldauf & Deubel, 2007) showing that the discrimination performance at goal positions is superior as compared to irrelevant and intervening positions. The results are evidence for the assumption that several movement-relevant goals are attended by spatially distinct foci while intermediate, movement-irrelevant locations are not selected. The parallel selection of several parts of the visual field during movement preparation may be spatially rather accurate and specifically restricted just to certain objects of relevance. In our experimental design the intermediate position between the two movement goals were non-targets in the sense that they had to be avoided during the sequence production. Such non-targets may remain unselected since they are at a higher risk of interfering with the action goals.

Interestingly, the findings are inconsistent with previous results by Heinze and collegues who suggested that attention can not be divided into multiple distinct foci (Heinze, Luck, Munte, Gös, Mangun & Hillyard, 1994). In their ERP-study they instructed the participants to attend to two out of four locations and to compare visual stimuli that were presented at these positions. In a blocked design, the two attended positions could be either adjacent to each other or separated by an intervening position that had not to be attended. In rare interleaving trials a dot probe was presented at any of the four positions. The N1-component evoked by these visual transients differed in dependence of whether or not the location where it was presented had to be attended. However, if the dot probe appeared at an irrelevant intervening position right between the two locations that had to be attended by the subject the evoked sensory responses was not suppressed but was equally enhanced. This suggests that attention formed an unitary region of space that may be adjusted as to cover multiple locations of interest, according to the task demands.

One possible explanation of the conflicting results regarding the selection of intervening locations might be that only during the preparation of movements the required selection of goal positions is more specific and accurately bound to goal objects. It may be speculated that the preparation of precise pointing movements poses higher demands on the spatial resolution of the involved selection processes as compared to instructed attention shifts in mere perceptual tasks (as in the task of Heinze et al.).

3.4.4 Neural correlates

In this study we found that early ERP-components in response to visual transients were modulated by the preparation of goal-directed hand movements. The modulation of the evoked N1-components most likely arose from enhanced processing of movement-relevant information in early visual areas. Therefore, we propose that this modulation reflects the result of attentional top-down signals, what selectively bias early stages of visual processing, rather than it represents brain activity involved in the movement programming, which provides the source for such attentional signals.

The obvious question arises where in the brain the top-down signals may originate. Several cortical structures are possible candidates to provide such attentional top-down signals for sequential movement preparation. Certain motor-related structures in frontal cortex are known to be involved in the long-term storage of multiple movement parts as well as in the crucial temporal ordering of various movement components during sequence planning (Ohbayashi, Ohki & Miyashita, 2003; Ninokura, Mushiake & Tanji, 2003, 2004; Averbeck, Chafee, Crowe & Georgopoulos, 2002; Averbeck & Lee, 2007). Mushiake and colleagues recorded from neurons in the lateral prefrontal cortices (PFC) of monkeys that navigated by stepwise cursor movements through a maze on the screen. During the movement preparation, various PFC neurons encoded the directions of all forthcoming cursor movements, even if there were considerable delays between all movement steps (Mushiake, Saito, Sakamoto, Itoyama & Tanji, 2006). Also the supplementary motor area (SMA) and the premotor area (PMA) are supposed to code for several movements ahead (Tanji & Shima, 1994; Shima & Tanji, 2000).

Nevertheless, one may argue that many of these frontal structures are unlikely to directly provide attentional signals to visual areas, since many of them encode movement directions with respect to the actual hand position rather than they code for goal locations in eye-centred coordinates. In the dorsal part of PMA, for example, neurons encode reach goals with respect to the eye and hand (Pesaran, Nelson & Andersen, 2006). Representations in such complex, non eye-centred frames of reference would require first back transforming the information in order to facilitate perception at certain positions that are retinotopically coded in early visual areas.

On the other hand, the posterior regions of parietal cortex (PPC) are known to play an important role in shifting spatial attention. In humans lesions to the PPC cause disorders in the representation of space (e.g., neglect). Also the planning and execution of goal-directed movements is often affected by injuries of the PPC (e.g., limb apraxia and optic ataxia, see Balint, 1909). More specifically, in monkey PPC several substructures have been identified that provide multiple representations of space for different kinds of actions (e.g., Andersen, Snyder, Bradley & Xing, 1997; Snyder, Batista & Andersen, 2000). While the lateral intraparietal area (LIP), for example, is crucial for the generation of saccadic eye-movements, the nearby parietal reach region (PRR) shows spatially selective activation before reaching movements. Andersen and colleagues interpreted the activity of PRR neurons as the encoding of reaching intentions (Buneo & Andersen, 2006). In general, the effector-specific and eye-centred neuronal coding in PRR would be the most likely source for attentional signals that could facilitate visual perception at the reach goal via feedback loops. Indeed, in a recent study, Baldauf, Cui & Andersen (2007) recorded from single neurons in the parietal reach region of two monkeys while the animals were preparing for a double reach task to two goal locations. They found first evidence that neuronal populations in PRR encode in parallel multiple movement goals of a planned hand movement sequence. This eye-centred planning activity in the parietal cortex may be the source of attentional top-down signals that directly cause enhanced visual processing of multiple goal positions.

4 Visual attention during the preparation of bimanual movements

ABSTRACT

We investigated the deployment of visual attention during the preparation of bimanually coordinated actions. In a dual-task paradigm participants had to execute bimanual pointing movements to different peripheral locations, and to identify target letters that had been briefly presented at various peripheral locations during the latency period before movement initialisation. The discrimination targets appeared either at the movement goal of the left or the right hand, or at other locations that were not movement-relevant in the particular trial. Performance in the letter discrimination task served as a measure for the distribution of visual attention during the action preparation. The results showed that the goal-positions of both hands are selected before movement onset, revealing a superior discrimination performance at the action-relevant locations (Experiment 3.1). Selection-for-action in the preparation of bimanual movements involved attention being spread to both goal locations in parallel, independently of whether the targets had been cued by colour or semantically (Experiment 3.2). A comparison with perceptual performance in unimanual reaching suggested that the total amount of attentional resources that are distributed over the visual field depended on the demands of the primary motor task, with more attentional resources being deployed for the selection of multiple goal positions than for the selection of a single goal (Experiment 3.3).

4.1 Introduction

The coordinated use of both hands is a key motor skill in primates. From an evolutionary point of view, it is the likely basis for the development of many cognitive functions like gesturing or the effective use of tools (Wiesendanger, 1999), and the advantages bimanual skills had in coping with the daily demands in hominids' life presumably caused the upright stand of man (Festinger, 1983). Many of the daily actions we perform involve the simultaneous coordination of both hands. In previous studies it has been shown that the movement patterns of both hands are highly synchronized and well aligned with each other. For example, the movements of the left and right hand begin and end at approximately the same time, although they may have different amplitudes (Kelso, Southard & Goodman, 1979a,b). Further, several studies showed that there are strong performance limitations during bimanual movements. To some extent this seems to cause problems in the planning or execution of independent movements with both hands at the same time (Diedrichsen, Ivry, Hazeltine, Kennerley & Cohen, 2003). This is not only true for timing constraints in performing complex polyrhythm in cyclic bimanual coordination tasks like bimanual finger tapping or pendulum swinging by the hands (Schoener & Kelso, 1988; Kelso, 1995). In addition there are also spatial constraints (Franz, Eliassen, Ivry & Gazzaniga, 1996; Swinnen, Dounskaia, Levin & Duysens, 2001; Lee, Almeida & Chua, 2002). Nonsymmetric actions with different spatial characteristics for the left and the right hand sometimes give rise to prolonged latencies (Spijkers, Heuer, Steglich & Kleinsorge, 2000; Spijkers, Heuer, Kleinsorge & van der Loo, 1997; Spijkers & Heuer, 1995; Franz, Eliassen, Ivry & Gazzaniga, 1996), and cause high error rates or distorted trajectories (Franz, Zelaznik & McCabe, 1991). These effects were traditionally explained by interferences during the motor programming (Rosenbaum, 1980; Rosenbaum & Kornblum, 1982) or, more recently, by conflicts during the selection of the appropriate response or of the stimulus-response mapping (Diedrichsen, Hazeltine, Kennerley & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley & Cohen, 2003).

Aside from these interesting findings of interferences during asymmetrical movements with the left and right hand, commonly performed bimanual movements in which both hands are used in a very orchestrated manner also pose a challenge to the cognitive system. For example, when bimanually grasping for an object, two spatially distinct contact points for the left and the right hand have to be prepared. In order to plan such a visually guided action the relevant visual information about the operandum has to be processed effectively. The mechanism of selective visual attention plays a prominent role in filtering the information about movement-relevant parts of the scene from other distracting visual input. As Allport (1987, see also Neumann, 1987) pointed out, visual selection in action preparation is a fundamental function of the attentional system. Accordingly, the premotor theory of attention describes how the intention to move an effector causes covert shifts of the attentional focus (Rizzolatti, Riggio & Sheliga, 1994).

It has been demonstrated for unimanual reaching movements that visual attention is deployed to the goal position well in advance of movement initialisation, and little room is left for the visual processing of action-irrelevant items in the visual field (Deubel, Schneider & Paprotta, 1998; Castiello, 1996). This resulted in the view that only one (action-relevant) object at a time is processed before the next goal-directed action. However, more recent studies have suggested that this picture may require some modification as soon as actions are considered which involve more than a single action goal. So, when the reach requires to avoid potential obstacles, attention seems to be flexibly distributed among several objects of interest (Deubel & Schneider, 2004). In the context of more complex (yet still unimanual) actions such as grasping for an object, Schiegg, Deubel and Schneider (2003) observed attentional effects that specifically facilitated visual processing at the two grasping points, i.e., at those parts of the object where thumb and index finger were going to contact the surface. Finally, our studies on the preparation of movement sequences showed that the visual system does not select only a single goal position of the impending very next movement, but that up to three goals of the subsequently performed reaches are selected even before the first movement starts (Baldauf, Wolf & Deubel, 2006; Baldauf & Deubel, 2007).

Also, little interest was paid until recently to the spatial selection of multiple goal position in actions that involve more than a single effector. In the case of bimanual actions, when contact points for the left and right hand have to be selected, the visual processing of both goal locations may be enhanced. Riek and colleagues (Riek, Tresilian, Mon-Williams, Coppard & Carson, 2003) tracked gaze position during the execution of precise bimanual aiming movements. They described how eye gaze shifts in the end phase of the reach from one target to the other in order to serially correct for spatial end-point errors of the left and right hand. This kind of overt allocation of visual attention may play a major role in the appropriate use of visual feedback, helping to minimize the spatial error that accumulates during the transport phase of the movement (Riek, Tresilian, Mon-Williams, Coppard & Carson, 2003). However, programming of the transport of both hands towards the two targets may also involve covert selective processing – well before the movement actually starts. So, the question arises whether the preparation of a bimanual action requires both target zones, at which the hands are intended to contact the object, to be attended before action initialisation. Indeed, the tight synchronization that is observed in the movement kinematics of both hands (see Kelso, Southard & Goodman, 1979a) may be an indication for a parallel pre-programming of both reaches, which may entail visual attention to be simultaneously deployed to both movement goals. Alternatively, attention may shift covertly back and forth from one goal position to the other while preparing for the coordinated action, in a manner as alike the serial overt attention shifts reported by Riek and colleagues (2003).

In a series of three experiments we studied the deployment of visual resources while participants prepared bimanual reaches to two distinct goal-positions in the periphery. Letter discrimination was used as secondary task in order to determine the distribution of visual attention during the planning phase. The analysis of discrimination performance in Experiment 3.1 and 3.2 revealed that when bimanual reaches are prepared, both goal positions are attended well before movement initialisation. This selection process involves the parallel allocation of visual attention to both target zones, and is not an artefact of the type of cue that was used to indicate the goal positions (Experiment 3.2). In Experiment 3.3 the participants performed unimanual reaches as primary task. The comparison of the discrimination performance under this condition with the performance in bimanual reaching suggests that the total amount of visual resources that is deployed in the visual field is not fixed but varies with the demands of the motor task.

4.2 Experiment 3.1

4.2.1 Methods

Participants. Six students of the Ludwig-Maximilians-University, aged between 24 and 27 years (three male), participated as consenting, paid volunteers in all of the following three experiments. They had normal or corrected-to-normal vision and were right-handed.

Experimental apparatus. Figure 4.1 provides a sketch of the experimental setup. The participant sat in a dimly illuminated room. The stimuli were presented on a 21-inch colour monitor (Conrac 7550 C21) at a frame frequency of 100 Hz with a spatial resolution of 1024 * 768 pixels. The active screen size was 40 x 30 cm. Pointing movements were executed on a slightly inclined plane in front of the participant. The use of a one-way mirror between the pointing plane and the participant's face allowed for free hand movements without visual feedback about the position of the hand and fingers. The mirror was adjusted such that the visual stimuli appeared to be projected onto the pointing plane. The luminance of the visual stimuli was adjusted to 23 cd/m^2. The stimuli were presented on a grey background, which was adjusted to a mean luminance of 2.2 cd/m^2. The moderate background brightness is important to minimise the effects of phosphor persistence (Wolf & Deubel, 1997). Effective viewing distance was 58 cm.

The movements of the left and right index fingers were recorded with a Fastrak electromagnetic position and orientation measuring system (Polhemus Inc., 1993), consisting of a central transmitter unit and two small receivers mounted on the tips of the participants' left and right index fingers. The sender unit was fixed 60 cm in front of the participant. The device allows for a maximum translation range of 10 feet, with an accuracy of 0.03 inches RMS. The frequency bandwidth of the system was 120 Hz, with a delay of 4 ms. Eye position was monitored by a video-based eye tracking system (Eyelink-I, SensoMotoric Instruments). An adjustable chin rest helped to reduce head movements. At the base of the chinrest, between the pointing plane and the participants trunk, two keys were placed to allow for the manual responses to the secondary discrimination task.

Stimuli and procedure. Figure 4.2 shows the stimulus sequence in a typical trial. The screen contained a continuously visible fixation cross at its centre and a star-like configuration of three crossing elements. The three elements had differently coloured margins (red, blue and green). At the six endings of this configuration white mask elements that resembled digital '8's were shown; they appeared at an eccentricity of

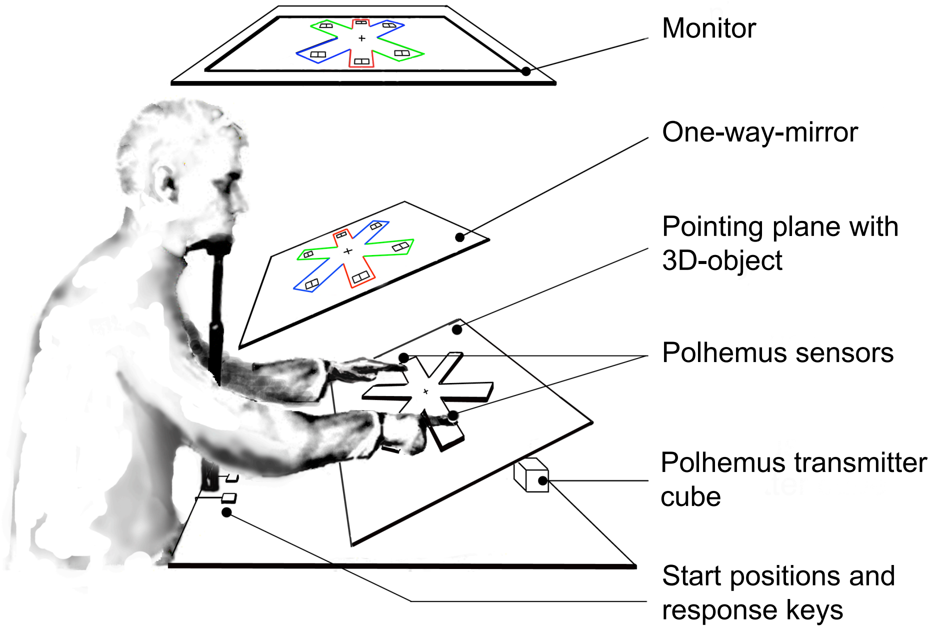


Figure 4.1: Experimental setup. The visual stimuli were generated on a video display and were projected via a half-translucent mirror onto a slightly declined pointing plane in front of the participant. The mirror was adjusted such that the visual stimuli appeared in the centre of the manipulation space. Movements of both index fingers were recorded with a Polhemus Fastrak electromagnetic tracking device. Eye fixation was controlled with a video-based eye-tracker.

7.2 deg. Their horizontal width was 0.90 deg of visual angle; their height was 1.40 deg. The visual presentation of the coloured star-like configuration corresponded to a real, 1 cm thick wooden object with similar shape and spatial extent that was mounted on the reaching plane. Therefore, whenever the participant reached for the visually presented configuration, he/she also obtained tactile information about the object. This helped to provide a more realistic interaction with the object, but without visual feedback about the finger positions during the reaching period. Also, the wooden object provided some tactile feedback about the accuracy of the reaches. The participants were required to fixate the central cross throughout the trial. At the beginning of each trial they positioned their left and right index fingers at the base of the chin rest. The distance between the hands' start positions and the reach goals was 24 deg of visual angle for the close goals, 31 deg for the goal positions on the horizontal (red) bar and 36 deg for the farthest goals (i.e., the upper ends of the tilted bars).

In each trial the participants had to perform a dual-task. The primary task was to perform bimanual reaching movements. The secondary task was designed to measure the deployment of visual attention and consisted in a letter discrimination task. Participants were asked to focus on the motor task, by encouraging them to react quickly and accurately. The perceptual task was stressed to a lesser extent, by explicitly informing the participants that they would quite often be unable to perceive the discrimination target.

After an initial delay of 600-1000 ms the central fixation cross was replaced by a small coloured dot (red, green or blue). The colour of the dot cued one of the three branches of the surrounding star configuration. Upon the appearance of this colour cue the participant had to perform a bimanual reaching movement to the mask elements at the endings of the cued branch.

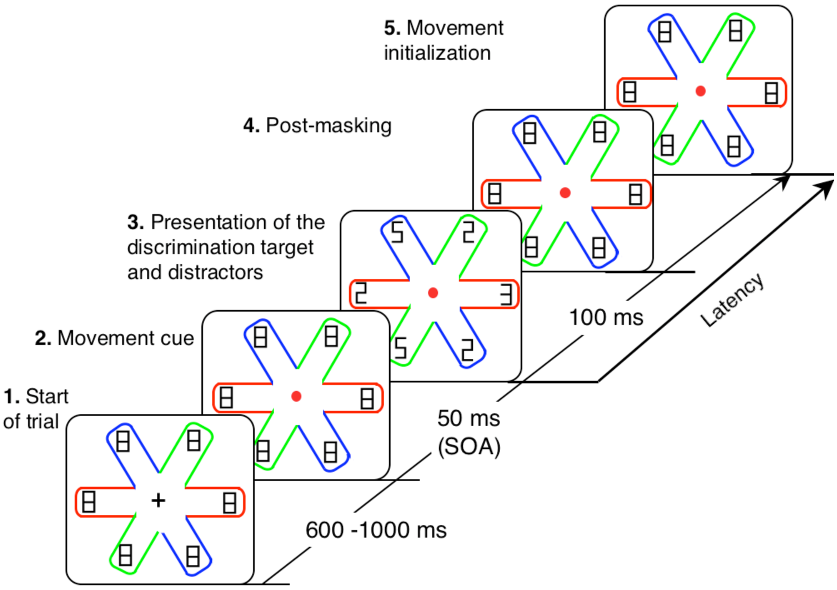


Figure 4.2: Sequence of stimuli in Experiment 3.1. After a random delay a centrally presented coloured dot cued the ends of one of the coloured branches of the configuration as the movements goals of the next bimanual reaching movement. After a SOA of 50 ms the premask characters changed into a critical discrimination target (resembling digital '3' or 'E') and distractors (resembling digital '2' or '5'). After a presentation time of 100 ms, all symbols were masked. At the end of each trial, the participant indicated by button press which of the two discrimination targets had been presented.

With a SOA of 50 ms after cue onset five of the six mask elements changed into irrelevant distractors (resembling digital '2' and '5'), while one randomly chosen mask element switched into a discrimination target (DT), resembling either a digital 'E' or '∃'. Distractors and discrimination target were presented for 100 ms and then changed back into mask elements, again resembling digital '8's. At the end of each trial the participant indicated, by pressing one of two buttons, which of both discrimination targets had been presented. This non-speeded response was given via two response keys mounted at the base of the chinrest. The next trial started with a delay of 1600 ms after the key-press.

Design. Each participant performed an initial training block of 108 trials which was not included in the data analysis. After the initial training, the participants performed five experimental blocks, each consisting of 108 trials. The coloured cue indicated the ends of either of the three branches as movement goals. DT was randomly presented at one of the six mask element positions and could be either a digital 'E' or '∃'. In total, this led to 36 different conditions (3 possible movement goal configurations * 6 DT positions * 2 types of DT). Each condition was presented three times in an experimental block. The conditions were selected at random in each trial.

Data analysis. The positions of both index fingers were stored together with the eye movements during the sessions on a PC and evaluated off-line by custom software. In order to determine latency, amplitude, and duration of the finger movements, an off-line program searched the movement traces for the points in time when the vectorial velocity reached a threshold of 10 mm / s (which is equivalent to about 1deg / s). The beginning and end of the pointing movements were calculated as linear regressions in a 50 ms time window around these threshold points. The program also analysed the data from the eyetracker and computed the spatial and temporal parameters of eventual saccades.

In order to ensure that the discrimination target was no longer present when the actual movement started, trials with onset latencies of the initial movement below 150 ms (equivalent to 50 ms SOA plus 100 ms presentation time), were excluded from further analysis. We also discarded trials where movement onset latency was above 600 ms, or where the program detected a saccade or a deviation from eye fixation that exceeded 2 deg. Trials in which the pointing goal of the left or right hand was missed by more than 3 deg or the movement was erroneously executed toward a non-cued pair of pointing goals were classified as pointing errors and were not analysed further.

The accuracy of the perceptual performance can be expressed by the percentage of correct decisions on the identity of DT; since there were two alternatives, chance level was at 50%. For the analysis of perceptual performance in relation to the movement task, we computed percent correct discrimination as a function of the position of the discrimination targets with respect to the movement targets (MT) in the particular trial. Two conditions were of special interest: (1) DT was presented at one of both movement goals, or (2) DT appeared at any of the remaining four character positions that were movement-irrelevant because they were not a movement goal in the particular trial.

Statistical analyses in this and the following experiments were performed with the 'R' statistical package (Ihaka & Gentleman, 1996) and included repeated-measure analyses of variance. Post-hoc comparisons were done with t-tests.

4.2.2 Results

Discarded trials. 6.0% of all trials in this experiment were discarded because the movement latencies were too short (see Table 4.1). In these trials, the presentation of the discrimination target had not yet been masked by the time the reach was initialised. In another 4.5% of trials movement initialisation was delayed by more than 600 ms - these trials were excluded because movement latencies were too long. 1.0% of trials were discarded because saccadic eye movements or other significant deviations of central fixation occurred. Finally, in 9.0% of trials one movement goal was missed by more than 3 deg of visual angle. These trials were also excluded from further analysis. Movement performance. Figure 4.4a shows the endpoints of the bimanual reaches for all six participants, demonstrating that the pointing movements were performed quite accurately. The mean spatial distance between the instructed left target and the landing positions of the left hand was 0.78 deg (SE = 0.03 deg). The accuracy of the right hand was slightly superior with a mean spatial error of 0.69 deg (SE = 0.02 deg). Figure 4.3 shows some exemplary trajectories of the bimanual reaches of one participant.

The bimanual reaches were initialised after 231 ms on average (see Table 4.1). Both hands moved in a coordinated fashion and were well synchronized in initialisation. There was no significant difference between the left and right hand in respect of movement latency, nor in movement durations (for an overview over the movement parameters see Table 4.1). In 2/3 of the trials, namely, when the blue or green branches of the configuration were cued, the movement goals for the left and right hand appeared at different distances from the starting position. For instance, if the green, right-tilted bar was cued the left hand had to reach shorter (24 deg of visual angle) than the right hand (36 deg). We analysed the movement latencies and durations for those subset of trials, in which the goal distances for both hands differed. Movement latencies did not significantly differ between reaches to distant versus close goals, with means of 228 ms (SE= 11.4 ms) and 230 ms (SE= 11.3 ms), respectively. However, the reaches to distant goals took on average 70 ms longer than those to close-by goal locations (346 ms versus 417 ms, $t(5) = 3.89$, $p < .012$). The mean vari-

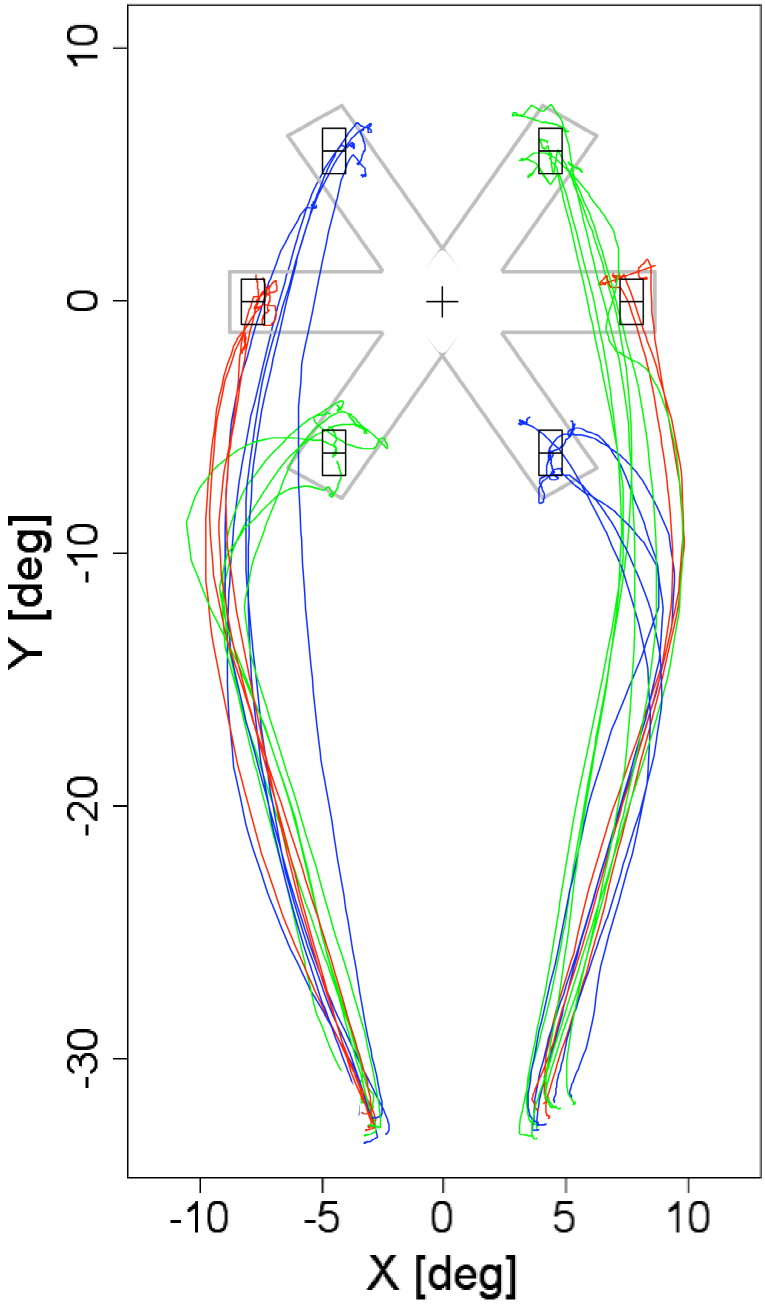


Figure 4.3: Typical movement trajectories of a single participant. The colours (red, green and blue) indicate the trajectories that were executed towards the respectively coloured parts of the configuration.

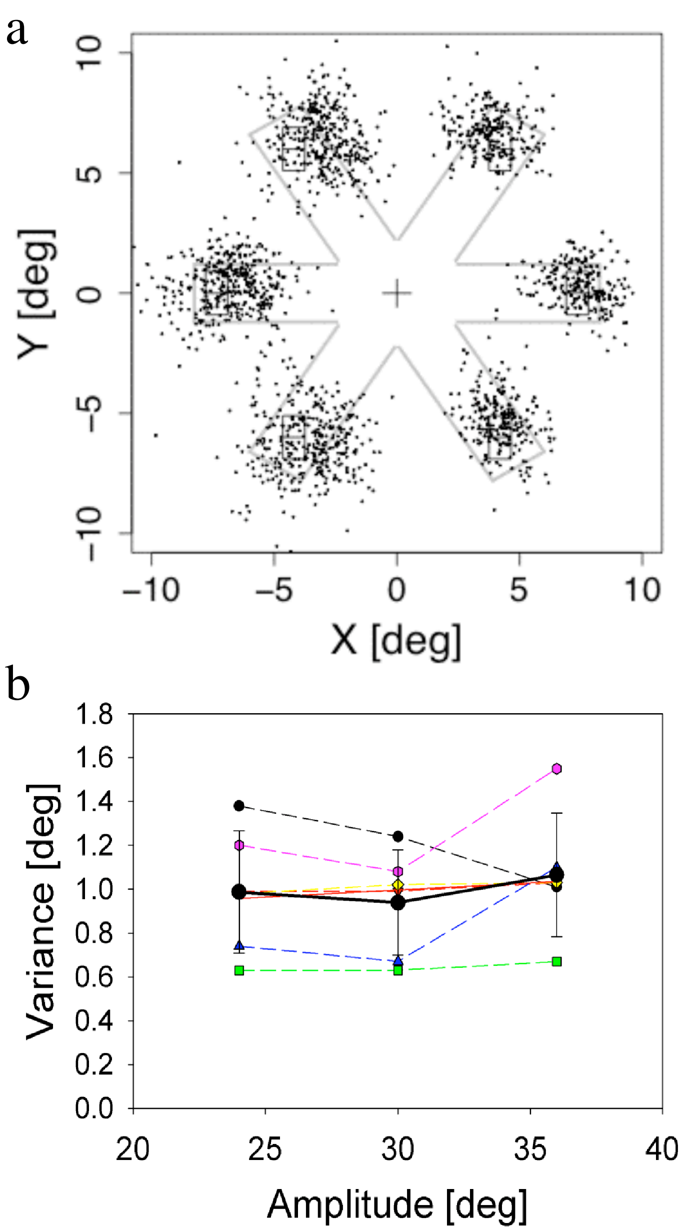


Figure 4.4: **(a)** Final landing positions of the left and right index finger in bimanual reaching movements of Experiment 3.1. **(b)** The spatial variance of the reaching amplitudes as a function of the distance of the reach goals from the starting position. The dashed lines represent the values of the six participants; the solid line indicates the means across the participants.

ances of the amplitudes of reaches to distant versus close goals were rather similar (1.07 deg for far reaches and .99 for short reaches, see Figure 4.4b). An one-way ANOVA revealed no significant main effect of the reaching distance (levels 'far', 'intermediate', 'near') on the variance of the respective movement amplitudes, $F(2, 10)= .98$, $p> .4$.

	Exp 1	Exp 2a	Exp 2b	Exp 3
Task:				
Primary task	bimanual reach	bimanual reach	bimanual reach	unimanual reach
Secondary task	singe letter discr.	letter comparison	letter comparison	singe letter discr.
Discarded data:				
Eye-movements	1.0 %	0.5 %	1.8 %	0 %
Too short latency	3.3 %	4.0 %	2.1 %	0.1 %
Too long latency	0.3 %	0.4 %	0.5 %	4.3 %
Movement parameters:				
Left / Right hand:				
Latency left hand [ms]	227 (11.9)	231 (15.8)	272 (22.1)	440 (23.9)
Latency right hand [ms]	236 (12.9)	250 (19.6)	280 (20.4)	444 (20.6)
Duration left hand [ms]	401 (9.2)	426 (13.4)	411 (10.4)	400 (13.5)
Duration right hand [ms]	393 (11.1)	413 (13.3)	405 (12.1)	396 (12.5)
Reach accruracy left [deg]	0.78 (0.03)	0.91 (0.07)	0.76 (0.02)	0.83 (0.02)
Reach accuracy right [deg]	0.69 (0.02)	0.66 (0.02)	0.92 (0.05)	0.62 (0.02)
Far / short reaches:				
Latency far reaches [ms]	230 (11.3)	248 (18.8)	275 (20.8)	457 (32.4)
Latency interm. reaches [ms]	231 (12.1)	251 (19.4)	280 (21.2)	452 (35.3)
Latency short reaches [ms]	228 (11.4)	250 (19.9)	276 (20.7)	455 (30.5)
Duration far reaches [ms]	417 (14.3)	400 (19.9)	420 (9.7)	395 (11.6)
Duration interm. reaches [ms]	387 (12.5)	393 (22.1)	393 (10.6)	359 (12.8)
Duration short reaches [ms]	346 (11.4)	318 (12.2)	385 (10.2)	340 (9.2)

Table 4.1: Percentage of trials that were discarded due to various criteria in each of the four experiments. The lower part lists the observed latencies and durations of the left versus right hand as well as the respective movement accuracy (means and standard errors).

Additionally, we wanted to assert that the presentation of the discrimination target at certain positions relative to the movement goals did not specifically interfere with the movement initialisations. Since the letter discrimination task is supposed to be a measurement of attention during the movement initialisation, the presentation of the discrimination target at a goal position should not prolong or shorten the latencies of the intended reach in comparison to reaches that were aimed at positions where no discrimination target was presented. An one-way ANOVA indeed showed no significant effect of the factor 'DT position' on the latency of the left or right hand (F(2, 10) = 2.23, p> .16 and F(2, 10) = .53, p> .60, respectively), nor on the duration of the movements of the left or right hand, F(2,10) = .64, p> .54 and F(2,10) = .86, p> .45.

Perceptual performance. The accuracy with which participants identified the discrimination target at any of the six mask positions served as the measure of the spatial allocation of attention before the onset of the bimanual reach towards two goals. Figure 4.5 represents the discrimination performance as a function of the relative position of the discrimination target with respect to the movement targets. The discrimination performance was close to chance level if DT was presented at any position that was movement-irrelevant in that particular trial (condition 'other'), with a pooled performance level of 53 % correct (SE=3.7 %). In contrast, perceptual discrimination was superior at the movement target locations of the bimanual reaches with 69% (SE= 5.3%) correct discriminations (68% at the right vs. 70% at the left MT).

A one-way ANOVA showed a significant effect of the factor relative position of the discrimination target ('DT-position', with the levels 'DT at left MT', 'DT at right MT' and 'other') on the performance in the letter identification task, F(2,10)=11.1, p<.002. Pairwise post-hoc comparisons showed that performance at the movement goals were significantly better than at the movement-irrelevant locations, t(5)= 4.28, p<.007 and t(5)= 4.58, p<.005, for the left- and right hand-side respectively. Perceptual discrimination performance was not significantly different at the left versus the right hand's goal, however, t(5)= 1.18, p >.28. Interestingly, discrimination performance was superior at the goals of the far reaches, i.e., at the upper ends of the blue (right-tilted) and the green (left-tilted) branches with on average 70% correct (SE=

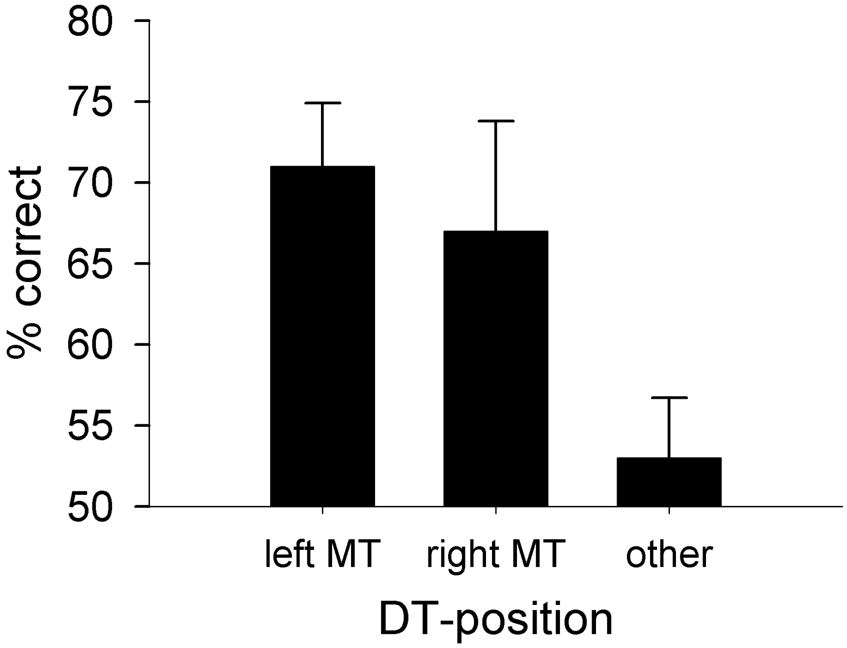


Figure 4.5: Discrimination performance in the letter discrimination task of Experiment 3.1. Data are presented as a function of the relative position of the discrimination target with respect to the cued movement goals. Vertical bars indicate standard errors.

5.2 %), in comparison to performance at the closer reach goals at the lower ends of the two tilted bars, with 62% (SE= 5.6 %) correct on average (t(5)= 2.02, $p < 0.05$, one-tailed). Performance values at the distant and the close reach goals were both significantly higher than at the task-irrelevant locations, t(5)= 4.03, $p < .01$ and t(5)= 3.08, $p < .03$, respectively.

4.2.3 Discussion

The results from this first experiment revealed significant benefits for perceptual processing at the movement goals of both the left and the right index finger, as compared to the discrimination performance at the locations that were movement-irrelevant in the particular trial, showing that the preparation of a bimanual reach movement leads to improved visual perception at both intended movement goals. However, an alternative explanation for this finding is that the participants may have attended to the left-hand side in some trials and to the right-hand side in other trials. By averaging across the individual trials this would lead to a similar pattern of aggregated results. Experiment 3.2 will address this caveat in more detail and test whether both movement goals are indeed attended simultaneously in each trial.

When both effectors were directed to goals with different distances from the starting point, the hand that had to reach for the more distant goal terminated about 70 ms later than the other hand. The observed movement durations for distant, intermediate and close goals were in accordance with Fitts' Law (Fitts, 1954; Fitts & Peterson, 1964), predicting longer movement times for more distant targets. The variances of the movement amplitudes were approximately constant for the different movement amplitudes (see Figure **??**c). This indicates that the participants tried to land within the cued mask element, which is more difficult to achieve for the more distant locations. In Fitts' law, the difficulty of a movement is theorized to be a logarithmic function of the ratio of the target distance and its width (see Fitts, 1954; Fitts & Peterson, 1964). Thus, following Fitts' conceptualisation the distant goals in our paradigm have a higher 'index of difficulty' than the close ones.

This may be related to the finding that during movement preparation the more distant goals were significantly better attended than the close goals. The data suggest that the goal with the higher distance-to-width ratio (equivalent to a higher index of difficulty) is attended to a higher degree during the preparation period of a bimanual movement (see General Discussion).

4.3 Eperiment 3.2

The first experiment demonstrated that the movement goals of the right and left hand were both attended while preparing for a bimanual reach. This resulted in superior discrimination performance at each of these locations, as compared to the perceptual performance at the movement-irrelevant locations. The second experiment addressed whether attention was deployed to the reach targets in parallel or serially in time. In order to examine this question, we used a same-different matching task. This task required participants to compare two discrimination targets appearing briefly at different locations with each other. Since the short presentation time precluded serial attention shifts, the participants could successfully compare the target letters only if they were able to attend simultaneously to both locations. In accordance with others (e.g., Logan, 2005) we assume that a presentation interval of 100 ms is too short for participants to shift their focus of attention between the two positions (for a similar approach see Hahn & Kramer, 1998; Kramer & Hahn, 1995).

In a second version of this experiment (Experiment 3.2b) we used a numeric cue instead of a colour cue in order to assure that the visual facilitation found is a consequence of the movement preparation, rather than caused by the specific cue characteristics.

4.3.1 Methods

Participants, stimuli, and procedure. The same six students as in Experiment 3.1 participated. The procedure and the stimuli used were similar to the previous experiment except for the secondary task (see Figure 4.6). In Experiment 3.2a, the participants again performed bimanual reaches to the mask elements at the ends of the branch instructed by the colour cue. As secondary task participants now had to perform a letter comparison (match-mismatch) task. For this purpose two discrimination targets were shown simultaneously for 100 ms, replacing the two mask elements at the ends of one of the three coloured branches. During the presentation of the discrimination stimuli, the other elements switched into distractors (’2’s and ’5’s), as in the previous experiment. Discrimination targets and distractors were then masked by digital ’8’s. The particular branch on which the two discrimination targets appeared was chosen randomly. After performing the movement, participants indicated, by pressing one of two buttons, whether the two discrimination targets had been the same or different.

Experiment 3.2b was aimed at controlling for possible effects of the type of cue on selective attention. This experiment was similar to Experiment 3.2a except for the way the movement targets were cued. In this experiment, the star-like configuration was defined by a white outline instead of a multi-coloured contour. In order to define two mask elements on a particular branch as reach goals, a roman numeral (‘I’, ‘II’, or ‘III’) was presented at the central fixation point. If a roman ‘I’ was presented the participants were instructed to reach with both hands to the mask elements at the endings of the branch that was tilted to the right (i.e., the right upper and left lower

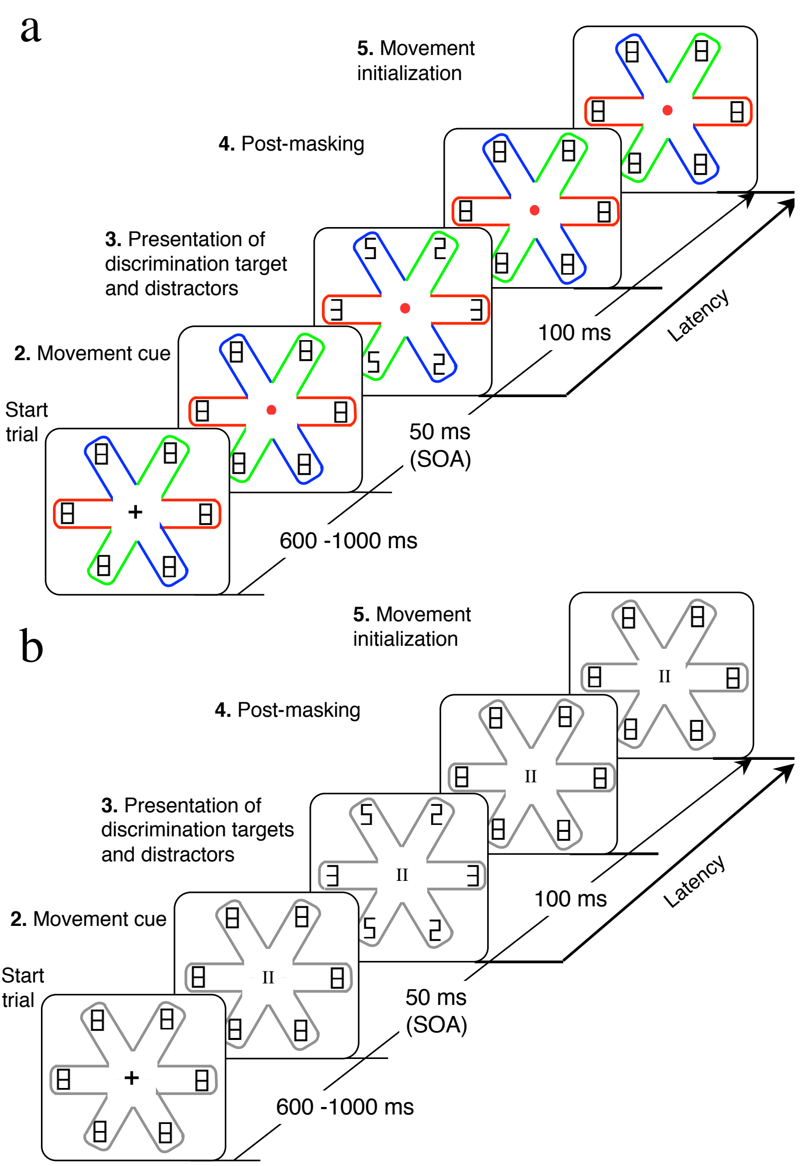


Figure 4.6: **(a)** Sequence of stimuli in Experiment 3.2a. The secondary task was a letter comparison task (match/mismatch-task). After a SOA of 50 ms two discrimination targets (each of them resembling either a digital ’∃’ or ’E’) were presented simultaneously for 100 ms only. **(b)** Sequence of stimuli in the Experiment 3.2b. Movement goals were cued by a central roman numeral.

mask element). In case of a roman 'II' they were instructed to reach to the ends of the horizontal bar. If a roman 'III' appeared they had to reach to the mask elements at the ends of the left tilted bar, i.e., to the left upper and the right lower mask element. Participants were instructed to reach as fast as possible after presentation of the central numeral. Design. Each participant performed four experimental blocks of Experiment 3.2a and four blocks of Experiment 3.2b, in an order balanced across the participants. Each block consisted of 108 trials. The central cue (colour or numeric, respectively) indicated the ends of one of the three branches as goal positions. The discrimination targets'E'and'Ǝ'appeared with equal probability. In half of the trials the discrimination targets were identical, in the other half of the trials they were different. Altogether, this led to 36 different conditions (3 MT positions x 3 DT arrangements x 2 types of DT x 2 types of DT equity); these conditions were presented in randomised order. The central movement cue had no predictive validity for the presentation location of the discrimination targets. Now, two experimental conditions were of special interest in the data analysis, indicating the location of the discrimination targets relative to the movement goal positions: The discrimination targets could either appear at the two positions that were cued as movement goals (condition 'DTs at MTs') or at two positions that were not movement goals in the particular trial (condition 'other').

4.3.2 Results

Movement performance. In Experiment 3.2a, 4.9% of trials had to be excluded from further analysis due to insufficient movement performance; 4.3% had to be excluded in Experiment 3.2b (for details see Table 4.1). In Experiment 3.2a, the mean spatial distance between the final landing position and the centre of the instructed movement targets was 0.83 deg (mean across both hands). Average latency of movement initialisation was 231 ms (SE= 15.8 ms) for the left hand and 250 ms (SE= 19.6

ms) for the right hand. The movement durations were similar to those observed in Experiment 3.1 (see Table 4.1). As can be seen from Table 4.1, the movement parameters in Experiment 3.2b (numeric movement cue) were very similar to those in Experiment 3.2a. Neither the mean latencies (t[5]= -2.6, p> .05) nor the movement durations (t[5]= 0.53, p> .60) differed significantly. Movement latencies were again analysed as a function of the position of the discrimination targets relative to the movement targets in order to assert that the movement performance was not affected by where the DTs were presented. The statistical analysis revealed that the latencies of the bimanual reaches were independent of the position of the discrimination target: Separate analyses of variance showed no significant main effect of the factor 'DT position' on the latencies, F(1, 4) = 0.011, p > .92, F(1, 4) = .0213, p > .89, nor on the durations of the movements, F(1, 4) = 0.0024, p > .96.

Perceptual performance. The solid bars in Figure 4.7 present the discrimination performance for two different relative arrangements of both discrimination targets with respect to the movement goals. If the discrimination targets appeared at movement-irrelevant positions, i.e., at the ends of a branch that were not movement goals in that particular trial, the comparison of both target letters failed and the participants performed at chance level (51 % correct). However, if the locus of discrimination target presentation coincided with the movement goals of the current trial, performance in the match-/mismatch comparison task improved to 63% correct comparisons. A t-test confirmed this difference to be significant, t(5)= 3.11, p< .027.

The striped bars of Figure 4.7 represent the discrimination performance in Experiment 3.2b where a roman numeral cued the movement goals in each trial. Target letters that had been presented at both reach goals were compared successfully in 65% of trials. If the discrimination targets appeared at movement-irrelevant positions, performance in the comparison task was close to chance level with 52 % correct

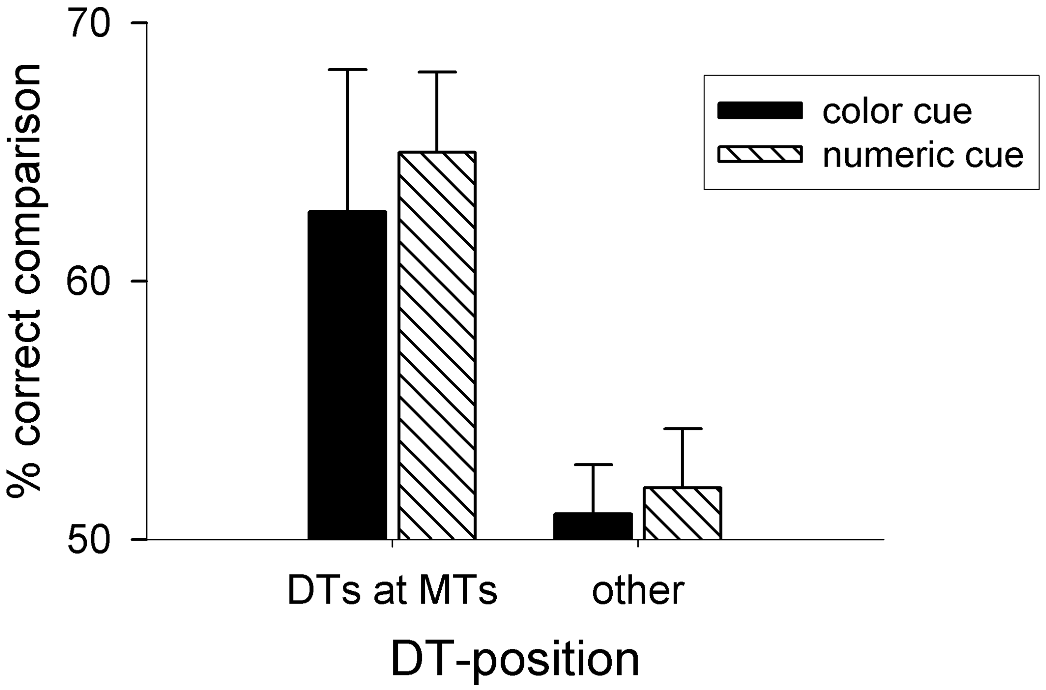


Figure 4.7: Perceptual performance in the letter comparison task of Experiment 3.2a (solid bars) and Experiment 3.2b (striped bars).

discriminations. A t-test confirmed that the difference between these two conditions was significant, t(5)= 3.94, p< .011. Importantly, performance in both versions of Experiment 3.2 did not differ significantly. T-tests confirmed a non-significant difference between the performance in both versions of the experiment, for both the condition 'DTs at MTs', t(5)= -0.30, p> .77, and the condition 'other', t(5)= -0.45, p> .67.

4.3.3 Discussion

The results of the letter comparison task in Experiment 3.2 provide evidence for the assumption that the preparation for a bimanual reach involves a parallel distribution of spatial attention to both movement targets. This rules out the alternative hypothesis that attention shifts serially between the reach goals in order to select information about the two goals of the index fingers, and that attention may have been deployed randomly to either action-relevant target in Experiment 3.1. Experiment 3.2b was designed to ensure that the effects were not caused by the use of a specific type of cue. The results suggest that the better visual processing at both goal positions does not result from the fact that both are surrounded by the cued colour but from the movement preparation. The intention to reach to both positions with the right and left hand causes the selection-for-action of the intended points of contact - independently of how the reaches are instructed.

4.4 Experiment 3.3

In this final experiment participants were asked to perform unimanual reaches with either the left or the right hand. It is important to compare the distribution of attention during the preparation of bi- and unimanual reaches for at least two reasons. Firstly, we wanted to exclude an alternative interpretation of the results obtained so far. It may be argued that attention is deployed to both locations not because both are the movement goals for the right and left fingers, but because these locations are perceptually grouped since they belong to the same object part, e.g., the horizontal bar (Duncan, 1984). Following this line of argument, the preparation for a reach to a single mask element - either the left or the right one – may have been sufficient to facilitate processing of the whole object part. Alternatively, only those goal locations may be selected that are relevant for the planned action. If this is true the preparation of unimanual reaches should result merely in unilateral facilitation.

A second aspect was to compare, within the same participants, the overall perceptual performance in the two different tasks. It is a widely accepted assumption that there is a constant capacity of visual resources, which are distributed by the mechanism of selective attention (see, e.g., Bundesen, 1990; Bundesen, Habekost & Kyllingsbaeck, 2005). This implies that when two targets have to be selected in parallel (as for a bimanual reach), perceptual performance at each target location should be inferior to perceptual performance at the movement target when just one goal-location is action-relevant (as for the unimanual reach).

4.4.1 Methods

Participants, stimuli and procedure. The same six students as in the previous experiments participated in this study. Stimuli and procedures were the same as in Experiment 3.1 except for the primary motor task. Simultaneously with the presentation of the colour cue that indicated one of the branches as action target, an acoustical cue indicated whether the participant had to reach with the left or the right hand. The goal for the left or right hand reach was defined as the ipsilateral mask element on the cued branch. If a high-frequency beep accompanied the colour-cue, the participant had to reach with his / her left hand to the left-sided mask element of a particular branch. If a low-frequency beep was presented, the participant had to move his / her right hand to the respective mask element on the right-hand side of the branch. The participants were asked to perform the reaches as fast and as accurately as possible.

Design. Every participant performed four experimental blocks, each consisting of 144 trials. The coloured dot at the centre cued one of the three branches of the wooden cross. The acoustic signal could be either a high- or low-frequency beep specifying to use either the left or right hand. The discrimination target (DT) was randomly presented at one of the six mask element positions and could be either an'E'or a '3'. In total, this led to 72 different conditions (3 movement goal configurations x 2 possible effectors x 6 DT positions x 2 types of DT). Each condition was presented two times in an experimental block. The conditions were selected at random in each trial.

4.4.2 Results

Movement performance. Table 4.1 provides an overview of the proportions of trials that had been excluded due to various criteria. In general the latencies and durations as well as the accuracy of unimanual reaches were similar to the corresponding parameters of bimanual actions in Experiment 3.1 and 3.2.

Perceptual performance. Perceptual discrimination was analysed with respect to three relevant conditions: (1) the location of DT presentation coincided with the movement target ('DT at MT'), (2) DT was presented at the location opposite to MT, but on the same branch ('opposite'), and (3) DT was flashed at any other position that was not on the branch the participant reached for ('other'). Figure 4.8 depicts the results of the perceptual task. As in the previous experiments discrimination performance was close to chance level if the discrimination stimulus was presented at a branch that was not relevant for the particular reach (condition 'other', 53% correct, SE= 1.9%). However, when the target was shown at the reach goal (as defined by the combination of the central colour-cue and the acoustic cue) discrimination performance improved to 75% correct (SE= 5.5%). Of specific interest in this experiment is the discrimination performance in those cases in which the target letter had been presented on the cued branch, but at the location opposite to the reach goal (condition 'opposite'). The data reveal that discrimination performance in this condition was as poor as at performance at the movement-irrelevant locations on the non-cued branches, with 52% correct decisions (SE=4.1%).

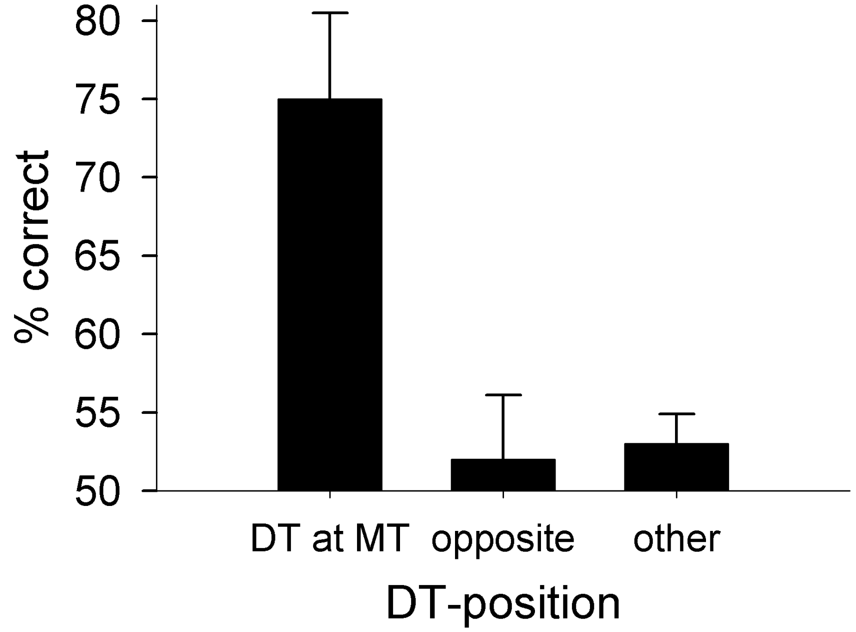


Figure 4.8: Discrimination performance in Experiment 3.3 (unimanual reaching) as a function of the relative position of the discrimination target with respect to the movement goal.

ANOVA showed a significant effect of the relative DT-position on the performance in the letter identification task, F(2, 10)= 8.82, p< .01. Planned contrasts showed that discrimination performance at the movement goal was significantly better than the pooled performance at other, non-cued locations, t(5)= 3.96, p< .011, and better than the performance at the opposite location of the cued branch, t(5)= 2.70, p< .04.

4.4.3 Discussion

The results of this last experiment have two important implications. First, they show that the attentional selection that occurs during the movement preparation period is spatially specific and limited to the movement-relevant locations. In the present paradigm the preparation for a single reach to only one end of a coloured bar did not lead to perceptual facilitation at the opposite end of the very same bar, demonstrating that attention did not spread across the whole object, or a particular part of the object. This is converging evidence that the processing advantages at multiple locations that we observed before in the bimanual reaches of Experiment 3.1 and 3.2 were a consequence of the intention to simultaneously move two effectors to two distinct goal locations, but did not result from perceptual grouping by a common same-coloured surrounding or from object-based attention.

Second, perceptual performance in the last experiment may be quantitatively compared to the performance in Experiment 3.1. In Experiment 3.3, the preparation for a unimanual reach caused an improvement in discrimination performance at the goal location from 53% at movement-irrelevant locations to 75% at the movement goal. A model that assumes a constant amount of resource would predict that this facilitation, which occurs before unimanual reaches, should be apportioned in case of preparation for bimanual movements and should therefore facilitate both goals in a less efficient manner. The discrimination performance at two goals for a bimanual reach is hypothesized to exceed chance level (0.5) to half the degree as performance at a single location did in case of unimanual reaches: $p' = 0.5 + 1/2 * (p - 0.5)$. Following such a model and given that the probability to correctly identify a discrimination target at a single intended reach goal equals $p = .75$ (unimanual reaches in Exp. 3), one would expect that discrimination targets at either goal of a bimanual action in Experiment 3.1 are identified with $p' = .62$. In Experiment 3.1, however, the participants prepared for a bimanual reach resulting in a perceptual facilitation of 69% (SE= 5.3 %) at the goal location of the right as well as the left hand goal (compared to again 53% at non-goals). This may indicate that the total amount of attentional resources that are distributed over the visual field may not be constant across both tasks.

4.5 General Discussion

4.5.1 Preparation of bimanual reaches involves allocation of attention to both goal locations.

In this study we used a dual task paradigm in order to probe the deployment of visual attention during the preparation of bi-manual reaches directed to two goals. Experiment 3.1 and 3.2 showed that both goal locations were attended before the movements were executed. At both goal locations the discrimination of target letters was significantly better than the discrimination performance at positions that were not goals for a reach in that particular trial. This main result is in line with previous studies on the involvement of visual attention in action preparation. It agrees with the general idea of the ‘premotor theory’ of attention (Rizzolatti, Riggio & Sheliga, 1994), which postulates that the programming of a movement causes attention to shift to the intended destination of the movement. Experimentally this has not only been shown for eye movements (e.g., Hoffman & Subramaniam, 1995; Deubel & Schneider, 1996) but more recently also for manual reaches. Deubel and colleagues (Deubel, Schneider & Paprotta, 1998; Deubel & Schneider, 2004) for example investigated how visual attention is shifted to the intended target location of a single hand movement. These former studies suggested that only one target is selected at a given point in time. Our study adds an important perspective to this ‘one-target-at-a-time’ conception. It provides novel and strong evidence for the notion that attentional shifts precede not only simple, singular reaches to one single goal but also more complex actions that involve multiple movements with several effectors towards various goals. If several locations are intended goals of a complex action, attention splits and facilitates visual perception at each of the goals. This happens at an early stage of action planning while the action is still in preparation. We therefore conclude that attentional facilitation is not restricted to a single location but can be flexibly distributed according to the demands of the motor task.

This matches the results of a recent study where we (Baldauf, Wolf & Deubel, 2006) demonstrated that attention also splits among multiple locations if participants intended to reach to these locations in a rapid sequence of hand movements. This suggests that the attentional system plans multiple steps ahead in time and is not restricted to facilitating only immediate goals.

4.5.2 Parallel selection of both reach goals.

Experiment 3.2 used a secondary match-/mismatch task. Participants had to decide at the end of each trial whether the two discrimination targets that were presented briefly during movement preparation either at the reach goals or at reach-irrelevant positions had been the same or different. In order to correctly perform in this secondary task both stimulus locations had to be attended. The discrimination targets were presented for only 100 ms and pre- as well as post-masked. The question arises here as to whether this time interval would allow for a serial shift of attention between both targets. There is substantial evidence in the literature that it takes at least 150 to 200 ms to first encode a spatial cue, then attend to the cued location, identify a stimulus at this location and subsequently reallocate attention to a another location in order to identify a second object. Logan (2005) provided an estimation of the time required to encode a cue and then to shift attention to a peripheral location. He argued that encoding the cue requires about 70 ms and that the subsequent attention shift to the cued location may take another 90 ms (see also Eriksen & Yeh, 1985; Kroese & Julesz, 1989; Madden, 1992). Ward, Duncan & Shapiro (1996) estimated that even up to 500 ms may be needed to shift attention endogenously to two peripheral positions. Therefore, in accordance with previous investigators (see also, e.g., Kramer & Hahn, 1995; Hahn & Kramer, 1998), we believe that 100 ms presentation time is too short to allow for serial shifts of covert attention between both goal locations. Given this conjecture, our findings demonstrate that participants simultaneously pay attention to both reach goals before they start the movement.

Our Experiment 3.3 showed that attention does not spread throughout the whole object part if only one end is intended to be reached by an unimanual hand movement. This means that the selection of both goal positions as observed in Experiment 3.1 and 3.2 results from the intention so reach to both goals rather than from any kind of perceptual grouping. Thus, our results strongly suggest that the preparation for a bimanual action involves the parallel distribution of visual attention to both the goals of the left and the right hand.

4.5.3 Manual and attentional asymmetries.

While there was no significant difference in movement initialisation times nor in movement durations between the left and the right effector, all four experiments revealed longer movement durations for reaches to more distant goals. This means that for the bimanual reaches the velocities of both hands were not re-scaled such as to result in synchronized movement termination. In fact, the farther reaches end on average 60 ms later than the reaches to the close targets. Therefore, our data are in line with the predictions of Fitts' Law – stating that the movement to a more distant goal takes longer than the aiming for a closer target (given that both targets have the same size) is not violated in our data. Since the width of the goals was kept constant in our paradigm, the difficulty of the reaches varied as a function of the goal's distance (see 'Fitts Law' in Fitts, 1954; Fitts & Peterson, 1964).

The finding of differing movement times contradicts some former studies reporting that in bimanual aiming movements of mixed difficulty the velocity of the reach with smaller difficulty (for example the reach with smaller amplitude) is rescaled in order to guarantee highly synchronized movement termination (see, e.g., Jackson, German & Peacock, 2002; Jackson, Jackson & Kritikos, 1999; Keele, 1986; Kelso, Putnam & Goodman, 1983; Kelso, Southard & Goodman, 1979b). Keele (1986) reported that the synchronization of both effectors occurs automatically even if the participants are not explicitly instructed to do so. Other studies investigating bimanual reach-to-grasp movements however did not find any evidence for movement synchronization (Castiello & Bennett, 1997; Castiello, Bennett & Stelmach, 1997).

The perceptual data of Experiment 3.1 demonstrate that these manual asymmetries were been accompanied by corresponding perceptual asymmetries before the movements started. The visual processing at both goal locations was significantly facilitated during the movement preparation, however with a strong and significant bias to better identify target letters at the goal of the farther reach. This provides some evidence that movement difficulty as defined in Fitts' law may be reflected in the amount of attentional resources deployed to the movement targets. If one of the intended targets is farther away from the starting point, it is more difficult to accurately reach towards this goal (given the movement goals are equally sized, see Fitts, 1954); this goes in line with a better perceptual performance at this location. The target difficulty (which is a function of the ratio of a goal's distance and its width) not only predicts the time it takes to reach for a certain goal but may also be a determinant for the relative attentional weight that is deployed to the goals before the movement starts.

4.5.4 Independence of the type of cue.

One critical argument against our interpretation of the data obtained in Experiments 3.1 and 3.2 may be that the observed facilitation in discrimination at the various goal locations does not result from the instruction as movement goals. Alternatively, the superior processing at these positions may be caused by the colour cue itself. The colour cue that indicated the goal locations in Experiment 3.1, 3.2a and 3.3 might also have a cueing effect independently of the movement goal instruction, in the sense that it facilitates perception on the whole same-coloured branch of the configuration. Some studies have shown that human observers can selectively attend to stimulus colour under certain conditions (e.g., Moore & Egeth, 1998). In visual search for example the prior knowledge of the colour of the search target can improve response speed and/ or response accuracy (Kapstein, Theeuwes & Van der Heijden, 1995). Also during eye fixation attention can be distributed to parts of the visual field on the basis of common features (see e.g., Saenz, Buracas & Boynton, 2002, 2003; Lu & Itti, 2005; Melcher, Papathomas & Vidnyanszky, 2005).

In order to rule out this alternative explanation we designed Experiment 3.2b which used a numeric cue to indicate the reach goals. It replicated the findings of Experiment 3.2a , suggesting that the intention to bimanually reach to the ends of a particular branch facilitates perception at the goal locations - independently of how the reaches are instructed. The view that the observed selective perception of movement-relevant parts of the scene is due to action strategies rather than common colour features of cue and targets is also supported in our last experiment in which participants performed unimanual reaches. Here the colour cue indicated one branch of the star-like configuration while an acoustic signal cued the effector to be used. The participants had to combine the colour and the acoustic cue in order to prepare the correct motor response. The data revealed that visual attention was then selectively deployed only to the reach goal of the respective effector (left or right side). If cueing in this last experiment had occurred by the common colour-feature (as opposed to movement instruction), the colour cue would have been effective for all positions on the same coloured branch, i.e., not only for the goal of the chosen effector but also for the location at the opposite ending of the same-coloured branch.

4.5.5 Bimanual actions involve more attentional capacities than unimanual actions.

A common assumption in the literature it that attention allows for the selective allocation of a limited (see, e.g., Cavanagh, 2004; Posner, 1978; Kahneman, 1973) and possibly constant amount of visual resources (e.g., Bundesen, 1990; Bundesen, Habekost & Kyllingsbaeck, 2005). For example, Posner (1978) stated that the system's 'efficient utilization for the processing of a signal code will usually reduce the efficiency with which it can process any other signal code'. Whether attention is focused on just one single object or broadly distributed among several items – the sum of attentional weights assigned to the various objects in the scene is assumed to be a constant (e.g., Bundesen, 1990; Bundesen, Habekost & Kyllingsbaeck, 2005).

The results of several recent studies have questioned this widespread assumption.

In a previous study, for example, we explored the attentional preparation of multiple goals of movement sequences (Baldauf, Wolf & Deubel, 2006). Here, a comparison of single- versus double- versus triple- reaches showed conflicting results: The more goals a motor sequence contained, the more resources were distributed before sequence initialisation. The attentional weight per goal stayed constant (e.g., at the first movement goal), whereas the overall amount of visual resources that were deployed in the visual scene increased with sequence length. Also a fMRI study by Chapman and colleagues (Chapman, Gavrilescu, Wang, Kean, Egan, & Castiello, 2002) found the BOLD activity in the posterior parietal cortex is increased if multiple potential targets are presented simultaneously, compared to a condition with only a single target. The authors claimed that the PPC activity that is related to a selection-for-action process may increase under conditions where the motor planning is more demanding.

Results like these are incompatible with a model of constant visual resources. Instead, they speak in favour of an alternative model of attentional deployment in action control: planning of a goal-directed movement recruits a certain amount of visual resources to process the intended goal, to such an extent as to grant a sufficiently successful execution of the motor response. Actions that involve multiple movement components or sub-movements flexibly recruit more visual resources and deploy these to the various targets. A possible interpretation of these findings is that the amount of attentional resources that are recruited depends on the specific task, such that they are used flexibly and economically to ensure the successful programming of the goal-directed movement(s).

Some results from the present study fit to this alternative view. When participants prepared for unimanual reach to a single goal position (Experiment 3.3) the secondary letter discrimination was selectively facilitated at this single goal location, yielding a discrimination performance of 75% correct (as compared to 53%at the other, movement-irrelevant positions). The preparation of bimanual movements in Experiment 3.1 also lead to selective deployment of attention to movement-relevant parts of the visual field. Here, however, discrimination performance was facilitated at both target locations to an significantly higher extent. This seems to indicate that the attentional resources that were deployed to prepare for a simple reach with one hand accreted when a bimanual action was required. So, there is no evidence in our data that attention is a limited and constant resource.

Conclusions. We explored the role of visual attention during the preparation of coordinated bimanual movements to two distinct goal locations. Our results demonstrate that well before the movements started both reach goals were attended in parallel. If both goals had different distances from the starting position more attention was deployed to the farther goal. In comparison to unimanual movements bimanual reaches seemed to recruit additional attentional resources. The results are in line with the view that complex movement preparation and selective attention are closely related.

5 Final Conclusions

The general aim of the present thesis was to explore the role of visual attention in the preparation of complex movements that involve multiple goal locations.

The three empirical studies presented in Chapters 2 - 4 employed different methodologies and experimental paradigms to explore the role of visual attention in the preparation of complex actions. By combining of psychophysics (Chapters 2 and 4) and electroencephalography (Chapter 3) we aimed to provide convergent evidence for the hypothesis that attention is flexibly adjusted to the requirements of movement planning.

One important difference to many other studies that investigated movement preparation is that the various paradigms used did not implement an artificial, i.e. instructed delay period (see, e.g., Medendorp, Goltz & Vilis, 2006; Eimer, Forster, Van Velzen & Prabhu, 2005; Chapman, Gavrilescu, Wang, Kean, Egan, & Castiello, 2002). Extensive delay periods are very common in fMRI studies (because of the temporal constraints of this method). Also in single-cell recordings delay or memory periods are used to disentangle the activity that arises from visual stimulation (e.g., the visual cueing of a goal position) and the activity that is prospectively associated with the programming of an upcoming movement (e.g., Andersen & Buneo, 2002; Andersen, Snyder, Bradley & Xing, 1997). Even many ERP studies on movement preparation employed instructed delay periods to better describe attention related components that occur rather late after cue onset (e.g., Eimer, Forster, Van Velzen & Prabhu, 2005). These approaches turn out to be difficult to interpret since the movement preparation is artifically prolonged and therefore the measured brain activity (or the attentional effects in psychophysical studies) can result from cognitive processes other than direct movement preparation.

The dual-task paradigms in Chapter 2 and 4, as well as the dot-pobe paradigm in Chapter 3 were designed to avoid the mentioned problems and test for the distribution of attention during the short period of natural movement latency (about 190-250 ms).

Another advantage of the present paradigms is that the effects of movement preparation on the visual processing at various movement goals were tested at the exact movement goal instead of nearby locations (in comparison to previous studies on movement sequences, e.g., Godijn & Theeuwes, 2003). For example, in the dual-task paradigms of Chapter 2 and 4 the movements had to be exactly directed to the mask elements that changed into the critical discrimination targets (similarly in Chapter 3). This allowed a higher spatial resolution in testing the distribution of visual attention over the visual field and made it possible to also probe visual processing at close-by non-target or intermediate positions.

The studies explored different types of complex action patterns such as movement sequences with various effectors (eye- or hand-movement sequences in Chapter 2 and 3, respectively) as well as simultaneous and coordinated movements with two effectors (such as bimanual reaches in Chapter 4). The required movements varied in their timing, some were simultaneously executed, others in a rapid sequence. Nevertheless, the preparation of all studied movement types shares common principles.

A common character of all instructed motor tasks was that they involved multiple goal locations to be directed to. The general finding was that multiple movement goals are selected during the preparation time period occurring before the movement onset.

This is especially remarkable for sequential movements such as saccade sequences in Chapter 2 or hand movement sequences in Chapter 3. When single movement parts to individual target locations are concatenated, spatial attention spreads along the intended path and the visual system selectively processes intermediate as well as final goals. All relevant visual information is gathered well in advance. The pre-planning of multi-step movement sequences involves the timely selection of relevant visual information that is crucial for sensorimotor transformations. This result is important because it helps explaining how the central nervous system can visually guide movements to several targets in a very fast sequence without interrupting the motor response or stepwise preparing for subsequent goals. At preparation stages as early as the analysis of sensory input, several movement components and the respective targets are incorporated in a common action plan in order to grant for a fluid execution of motor chains and efficient performance. The mechanisms of visual attention helps planning far in advance by selecting motor goals that lie in rather remote future (e.g., a third movement goal in the triple-sequences required in Experiment 1.2 in Chapter 2).

The preparation of several movement goals is not a sequential process. Rather the relevant visual information is gathered in parallel (see Experiments 1.3 and 3.2). The intention to move to several locations in space (either sequentially with one effector or simultaneously with different effectors) splits visual attention and flexibly adjusts it to various goal locations. This process involves distinct foci of attention as to cover non-contiguous regions in the visual field (see Experiments 1.1 and 2.2). These novel results contrast the former conception of selection-for-action as a mechanism that selects one target at a time (see, e.g., Deubel, Schneider & Paprotta, 1998; Deubel

& Schneider, 2004). Furthermore, the comparison between tasks involving a different number of movement goals (e.g., double- versus triple-sequences of saccades in Chapter 2, or uni- versus bi-manual reaches in Chapter 4) revealed the amount of visual resources distributed in the visual field not to be constant but to vary with the complexity of the required motor task. Similarly, the results in Experiment 3.1 showed that reach goals further away from the starting position need a higher attentional deployment as compared to close-by goals, indicating that the target difficulty (Fitts, 1954) of an to-be-reached object may influence the amount of attention is deployed to it during the movement preparation.

In natural tasks the performance in manipulating objects (for some examples see Mennie, Hayhoe & Sullivan, 2007; Droll, Hayhoe, Triesch & Sullivan, 2005; Triesch, Ballard, Hayhoe & Sullivan, 2003; Hayhoe, Shrivastava, Mruczek & Pelz, 2003) would arguably benefit from the parallel deployment of covert visual attention to several regions of interest even in conditions where eye movements are not restricted. Since the eyes can be only serially redirected, the parallel deployment of covert attention could be helpful in selecting multiple relevant locations. In many complex natural tasks certain relevant parts of the scene can not be fixated because the eyes have to be directed to other important movement components. In such cases, eye movements and parallel, covert shifts of attention may complement one another.

Regarding the neurophysiological implementation of the attentional system (see Chapter 1.4) it is interesting to notice that the manner, in which attention is distributed before complex movements, is very similar for movements of different effectors at study. For example, the results of Chapter 2, where attention was tested during sequences of eye movements, may be compared to the results in Chapter 3 studying sequences of manual reaches or to a previous study by (Baldauf, Wolf & Deubel, 2006) who used a very similar paradigm. It appears that the basic principles of attending to multiple movement goals, such as the parallelity or the non-selection of intermediate positions or the repeatedly observed gradient of attentional weights assigned to less important / subsequent goals, are independent of the effector system in use. This poses the question of whether the studied phenomena are the result of one central attention mechanism that serves as an input filter for any effector system. Alternatively, various parietal structures, which separately encode movement intentions for different effectors (see Chapter 1.4), may share common principles of how to weight relevant visual information and how to represent multiple goals The activity in these effector-specific planning structures of the posterior parietal cortex may have very similar effects on the processing of the incoming visual information.

Prospects. The results of the present studies also raise a variety of future research questions. A first one concerns the gradient of attentional facilitation at subsequent goals in a movement sequence as it was observed in two experiments of Chapter 2. In Experiments 1.1 and 1.2, the impending movement goal was selected more efficiently than the second one, and, subsequently, the second more efficiently than the third one. This pattern of results may be due to the increasing relative proximity to the first, cued position or, alternatively, due to the temporal order, in which the goals are reached. Future research should focus on the temporal order of motor sequences in order to disentangle the effects of temporal versus spatial constraints on the amount of attention that is deployed to the respective targets.

Attentional weighting is also of interest in situations where multiple objects , which are not targets per se, are taken into account for movement programming. For instance, if obstacles have to be avoided while reaching for a target attention may be split among the target position, the obstacle and the intermediate goals (such as the viapoints)? Similar to robots programmed to reach around an obstacle, humans may accomplish such a task by first guiding the hand towards an imagined intermediate goal aside of the obstacle and only afterwards continue to approach the target. Interestingly, superficial areas (Area 5 / 7a) of the the posterior parietal cortex also encode information about trajectories (Mulliken & Andersen, 2006).

A second line of experiments may further study the intermediate positions between two movement goals that are not selected or even inhibited. How will selection of these intermediate positions change in a sequential task, in which in the first place they are non-targets, but become a target at a later point of the sequence? One possibility to study this is to instruct triple-sequences, where the third movement component leads back to the immediate position between the first and second goal.

Further experiments could be conducted focusing on the similarities and differences in the preparation of different motor effectors. Does, for instance, attention spread over the path we want to walk? Parallel processing of spatial information is likely to play a crucial role in preparing for multiple footsteps in rapid order.

Also the neural basis of the underlying planning structures - a co-operation of frontal and parietal structures - needs additional empirical investigation. There is first evidence for complex, multiple-step movements to be encoded by parietal structures that are specialized in hand movements (Baldauf, Cui & Andersen, 2007). Is this also the case for other effector-specific structures?

There is a continuing debate on whether attention can or can not be split into non-contiguous foci and empirical evidence has been provided for both points of view. Two of the present studies demonstrated that attention does split in the specific case of movement preparation towards several goals. One possibility to resolve this ongoing debate may be to experimentally compare covert shifts of attention, which are involved in movement preparation towards multiple goals, with those attention shifts that occur in purely perceptual tasks. Is the splitting of the attentional focus a special-ity of attention-for-action? Preparing for accurate movements towards certain goals may require the selection of visual information to be more exact.

The results presented in Chapter 4 demonstrated that attentional selection does not always spread over an object of interest, as was found for the deployment of attention in purely perceptual tasks (Humphreys et al., 2005; Humphreys et.al., in preparation): Even for one object, the planning of goal-directed movements of the left and right hand towards certain points of application on the object can lead to a preferred processing spatially restricted to just these goal locations. Further questions arise, such as whether there are object-dependent attentional maps on the 3-D surface of to-be-grasped objects.

One minor finding in Chapter 4 also may inspire future studies. A more detailed analysis of the discrimination performance before bimanual reaches showed that more distant goals are selected more efficiently than near-by target locations. This strongly reminds the conceptualization of target difficulty in Fitts' Law (Fitts, 1954), which is a function of the reaching amplitude and target width: the more distant a movement goal is and/ or the smaller the target zone is, the higher is the index of difficulty of this movement target. These very first findings in Chapter 4 would nicely motivate follow-up studies, to analyze in detail the relationship of selection-for-action and target difficulty.

6 Appendix A. German summary / Deutsche Zusammenfassung

Beim Betrachten einer visuellen Szene wird nicht alle verfügbare Information gleichberechtigt verarbeitet und intern repräsentiert. Vielmehr ist die visuelle Wahrnehmung sehr selektiv. Ein Großteil der durch die Netzhaut eintreffenden Information wird bei der Verarbeitung ausgefiltert, um kognitive Ressourcen möglichst effizient einzusetzen. Was wahrgenommen wird ist stark von unseren Interessen und Handlungsintentionen beeinflusst. Besonders eindringlich wurde dies zum Beispiel in einem Experiment von Triesch, Ballard, Hayhoe & Sullivan (2003) demonstriert, das zeigte, wie leicht plötzliche Veränderungen in der visuellen Umgebung übersehen werden, wenn sie nicht gerade an Positionen geschehen, die für die aktuelle Aufgabe zu diesem Zeitpunkt besonders wichtig sind.

Visuelle Wahrnehmung ist kein passiver sonder ein aktiver Prozess. Sie wird fortwährend so angepasst, dass relevante Information bevorzugt verarbeitet wird. Die Selektion visueller Information erfolgt zum einen durch Augenbewegungen (Land & Lee, 1994; Land, 1998; Land, Mennie & Rusted, 1999; Hayhoe, Shrivastava, Mruczek & Pelz, 2003), die festlegen, welcher Ausschnitt der Umgebung auf die Netzhaut trifft. Zum anderen wird eintreffende Information durch den internen Mechanismus der verdeckten Aufmerksamkeit selektiert. Verdeckte Verlagerung von Aufmerksamkeit führt zu beschleunigtem Erkennen (Posner, 1980; Shulman et al., 1979), indem aufgemerkte visuelle Signale intern verstärkt werden (Mangun & Hillyard, 1987, 1988, 1990, 1991; Luck & Hillyard, 1995; Luck, Hillyard, Mouloua, Woldorff, Clark & Hawkins, 1994; Hawkins, Hillyard, Luck, Mouloua, Downing & Woodward, 1990; Henderson, 1996; Hillyard & Munte, 1984; Michie, Bearpark, Crawford, & Glue, 1987; Carrasco, Penpeci–Talgar & Eckstein, 2000). Dadurch können die Eigenschaften eines Objektes erfolgreich gebunden (Treisman & Gelade, 1980) und Gegenstände besser identifiziert werden (Eriksen & Hoffman, 1972; Müller & Rabbitt, 1989; LaBerge & Brown, 1989). In vielen Fällen reguliert die visuelle Aufmerksamkeit, welche Inhalte im visuellen Kurzzeitgedächtnis gespeichert werden und später Verhalten steuern können (Duncan, 1984; Bundesen, 1990). Die Verlagerung visueller Aufmerksamkeit ist nicht immer ein willentlicher Prozess, sondern geschieht oft unbemerkt. Sie führt dazu, dass der Wahrnehmungs-prozess ständig von top-down Signalen beeinflusst wird und in einem behaviouralen Rahmen von Handlungsplänen und Intentionen stattfindet.

Eine besonders wichtige Rolle spielt visuelle Aufmerksamkeit beispielsweise bei der Vorbereitung zielgerichteter Bewegungen. Das Zentrale Nervensystem muss relevante visuelle Information, z.B. über die Lage des Ziels im Raum, in neuronale Befehlssignale für einen Effektor umwandeln. Aufgabenabhängige Selektion ist daher einer der ersten Verarbeitungsschritte bei der Programmierung ziel-gerichteter Bewegungen ('selection-for-action', siehe Allport, 1987; Neumann, 1987).

Selektion zur Handlungplanung

Mehrere Studien untersuchten verdeckte Verschiebung von Aufmerksamkeit bei der Vorbereitung von sakkadischen Augenbewegungen (Remington, 1980; Shepherd et al., 1986; Kowler et al., 1995; Hoffman & Subramaniam, 1995; Deubel & Schneider, 1996; Van der Stigchel & Theeuwes, 2005). Deubel et al. zum Beispiel verwendeten ein Doppelaufgabenparadigma, in dem Versuchspersonen eine Augenbewegung zu einem zentral angezeigtem Ziel hin ausführen mussten. Es zeigte sich, dass kurzzeitig präsentierte Buchstaben in der Peripherie signifikant besser erkannt wurden, wenn sie am intendierten Sakkadenziel präsentiert worden waren. Diesem Ergebnis zufolge wird vor Ausführung einer Augenbewegung Aufmerksamkeit an die geplante Zielposition verlagert. Auch die Vorbereitung von manuellen Bewegungen erfordert die Selektion des Zieles über den Mechanismus der visuellen Aufmerksamkeit. Einige Studien zeigten experimentell, dass zielgerichtete Handbewegungen verzögert oder abgelenkt wurden, wenn während der Vorbereitungsphase ein irrelevanter Distraktor im Feld aufblitzte, der automatisch Aufmerksamkeit auf sich zog (Tipper, Lortie & Baylis, 1992; Jackson, Jackson & Rosicky, 1995; Howard & Tipper, 1997; Tipper, Howard & Jackson, 1997; Tipper, Howard & Houghton, 1998). Deubel und Kollegen (Deubel & Schneider, 1996; Deubel, Shimojo & Paprotta, 1997; Deubel, Schneider & Paprotta, 1998) kombinierten zielgerichtete, manuelle Bewegungen mit einer perzeptiven Zweitaufgabe. Die Ergebnisse zeigten, dass die Fähigkeit, tachistoskopisch dargebotene Buchstaben zu erkennen an der geplanten Zielposition erhöht ist.

Neurophysiologie der Aufmerksamkeit

Räumliche Aufmerksamkeit moduliert bereits frühe Stadien der visuellen Verarbeitung. In Gehirnstrukturen, wie z.B. LGN, V1, V2 und V4, führt die Verlagerung visueller Aufmerksamkeit zu einer Erhöhung der Ruheaktivität von Neuronen, die ihr rezeptives Feld im aufgemerkten Bereich haben (O'Connor, Fukui, Pinsk, & Kastner, 2002; Li, Piech & Gilbert, 2004; Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999; Corbetta, Kincade, Ollinger, McAvoy & Shulman, 2000). Auch die Aktivität in höheren visuellen Arealen, wie z.B. MT, MST, IT und TEO, die mit der Verarbeitung von komplexer Bewegungsinformation bzw. mit Objekterkennung befasst sind, werden durch top-down Signale moduliert (Treue & Maunsell, 1996; Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999; Desimone, Moran & Spitzer, 1989, siehe Abbildung 1.1).

Desimone und Kollegen schlugen in ihrem einflussreichen biased-competition Modell einen Mechanismus vor, bei dem unterschiedliche Repräsentationen miteinander in Konkurrenz stehen und sich gegenseitig inhibieren (Desimone & Duncan, 1995). Wird eine Repräsentation durch top-down Signale verstärkt führt das automatisch zur Abschwächung anderer Repräsentationen. Die neural theory of visual attention (NTVA, siehe Bundesen, Habekost & Kyllingsbaeck, 2005) basiert ebenfalls auf einem biased-competition- Ansatz und beschreibt, wie verschiedenen Objektrepräsentationen parallel attentionale Gewichte zugewiesen werden. Mehrere Planungsareale kommen als Quelle attentionaler top-down-Signale in Frage. Verschiedene Studien identifizierten ein parieto-frontales Netzwerk, das die Verlagerung von Aufmerksamkeit im Raum steuert. Interessanterweise sind diese Strukturen nicht nur bei verdeckter Aufmerksamkeitsverschiebung aktiviert sondern spielen auch bei der Planung von Bewegungen eine wichtige Rolle.

Multiple Handlungsziele

Viele Studien, die Aufmerksamkeit bei der Vorbereitung singulärer Bewegungen untersuchten, kamen zu dem Ergebnis, dass nur das Handlungsziel erfolgreich selektiert wird und für die Verarbeitung anderer Objekte im Raum wenig Ressourcen eingesetzt werden. Dies führte zu der Konzeption eines Selektionsmechanismus, der stets nur ein Ziel selektiert ('one-target-at-a-time', siehe z.B. Deubel, Schneider & Paprotta, 1998).

In der alltäglichen Interaktion mit unserer Umwelt werden jedoch oft bei weitem kompliziertere Handlungen ausgeführt. Oft werden mehrere Bewegungen zusammengefasst und in sehr rascher Abfolge ausgeführt (siehe z.B. Baldauf, Wolf & Deubel, 2006; Godijn & Theeuwes, 2003). Bimanuelle Greifbewegungen erfordern, dass für beide Hände unterschiedliche Kontaktpunkte programmiert werden. Im Bereich der Auge-Hand-Koordination werden beide Effektoren oft zu unterschiedlichen Zielen geführt (z.B., Johansson, Westling, Bäckström & Flanagan, 2001; Mennie, Hayhoe & Sullivan, 2007). Thema der vorliegenden Arbeit ist die Selektion multipler Zielpositionen während der Vorbereitung komplexer Handlungen.

Visuelle Selektion bei der Vorbereitung von Sakkadensequenzen

Die erste der drei empirischen Studien behandelt die Verlagerung visueller Aufmerksamkeit bei der Vorbereitung von Sakkadensequenzen. In den Experimenten kommt ein Doppelaufgabenparadigma zum Einsatz. Die priorisierte Erstaufgabe ist es, Augenbewegungssequenzen zu zwei Positionen in der Peripherie auszuführen. Dafür wird am zentralen Fixationspunkt ein endogener Hinweisreiz dargeboten, der eines von zwölf umliegenden Maskenelementen indiziert. Auf Erscheinen dieses Cues hin musste die Versuchsperson so schnell und so genau wie möglich eine Augenbewegung zur indizierten Position machen und sogleich im Anschluss daran zum im Uhrzeigersinn übernächsten Element weiter springen. Um die Verlagerung der Aufmerksamkeit während der motorischen Vorbereitungsphase zu messen, wurde 50 ms nach Erscheinen des Cues an irgendeiner der umliegenden Positionen ein Zielbuchstabe (′E′ versus ′Ǝ′) dargeboten, während alle anderen Maskenelemente sich in Distraktoren (′2′ und ′5′) umwandelten. Nach 150 ms Präsentationszeit wurden alle Elemente postmaskiert noch bevor die Sequenz initialisiert worden ist. Am Ende eines jeden Durchgangs musste die Versuchsperson angeben, ob sie meint, ein ′E′

oder ein 'Ǝ' sei an irgendeiner Position dargeboten worden. Abbildung 2.1 fasst den experimentellen Ablauf graphisch zusammen.

Die Analyse der Erkennungsleistung zeigte, dass die Erkennungsleistung am ersten und zweiten Sakkadenziel signifikant erhöht war, während sie auf allen anderen Positionen auf Zufallsniveau lag (siehe Abbildung 2.3). Interessanterweise war die Erkennungsleistung auch auf der zwischenliegenden Position nicht über Rateniveau. Die Ergebnisse sprechen dafür, dass beide Augenziele vor Bewegungsbeginn bereits selektiert werden und sich der Aufmerksamkeitsfocus während der motorischen Vorbereitungsphase in zwei räumlich gertrennte foci aufspaltet. Ein zweites Experiment (Exp. 1.2) erforderte die rasche Ausführung von Triple-Sequenzen. Die Ergebnisse hier zeigten, dass sogar eine dritte Zielposition vor Beginn der Sequenz bevorzugt verarbeitet wird (siehe Abbildung 2.4). In einem dritten Experiment kam eine Vergleichsaufgabe zum Einsatz (siehe Abbildung 2.5). Es wurden nun zwei anstatt nur einem Diskriminationsziel dargeboten und die Versuchsperson musste als Zweitaufgabe am Ende des Durchgangs angeben, ob die präsentierten Symbole gleich (d.h. beide zeigen ein 'E' oder beide ein 'Ǝ') oder ungleich gewesen waren. Die Darbietungszeit war in diesem Experiment auf 60 ms beschränkt. Die Ergebnisse zeigten, dass der Vergleich beider Symbole nur möglich war, wenn beide auf den Bewegungszielen des aktuellen Durchgangs dargeboten waren (siehe Abbildung 2.6). Dies ist starke Evidenz dafür, dass beide Zielpositionen parallel aufgemerkt wurden (siehe auch Godijn & Theeuwes, 2003), da es nicht möglich ist, innerhalb von 60 ms den Focus der Aufmerksamkeit zunächst zu einem Ziel zu verlagern, um das erste Element zu erkennen, und dann auf das zweite Ziel zu verschieben, um auch dieses Element zu analysieren (Kramer & Hahn, 1995; Ward, Duncan & Shapiro, 1996; Hahn & Kramer, 1998; Godijn & Theeuwes, 2003; Logan, 2005). Als Gesamtergebnis der Studie in Kapitel 2 lässt sich demnach festhalten, dass vor Augenbewegungssequenzen zu mehreren Zielen alle Zielpositionen parallel aufgemerkt werden und sich dabei der Aufmerksamkeitsfocus aufteilt, so dass irrelevante Zwischenpositionen nicht selektiert werden.

Selektion mehrfacher Handlungsziele vor manuellen Zeigesequenzen

Die zweite empirische Studie in Kapitel 3 der vorliegenden Arbeit untersuchte die visuelle Selektion multipler Zeigeziele mittels eines 'Dot-Probe'-Paradigmas (siehe auch Mangun & Hillyard, 1990, 1991). Von den Versuchspersonen wurde ein Elektroencephalogramm abgeleitet, während sie auf einen Cue hin Zeigesequenzen zu zwei von drei möglichen Positionen ausführten. Während der Vorbereitungsphase, also nachdem der imperative Hinweisreiz präsentiert worden war und bevor der Proband mit der geforderten Bewegung begann, wurde ein aufgaben-irrelevanter Lichtreiz präsentiert (siehe Abbildung 3.2). Der Lichtreiz blitzte für 70 ms (SOA 150 ms) an einer der drei möglichen Positionen auf: entweder am geplanten ersten Zeigeziel (Bedingung '1st MT') oder am zweiten ('2nd MT') oder an der dritten Position, die im aktuellen Durchgang nicht Ziel einer Bewegung war ('irr'). Die Verarbeitung des irrelevanten Lichtreizes evozierte an okzipitalen Elektroden ein visuelles Potential mit ausgeprägter P1/N1-Komponente. Wie aus früheren Studien bekannt, ist die Amplitude der N1-Komponente ein physiologisches Maß dafür, wie viel Aufmerksamkeit auf der entsprechenden Position im visuellen Feld war, als der Lichtreiz geblitzt wurde (Mangun & Hillyard, 1987, 1988, 1990, 1991). Die Analyse der N1-Komponenten diente in dieser Studie dazu, die Verlagerung visueller Aufmerksamkeit bei der Bewegungsvorbereitung zu messen. Die Auswertung der ereigniskorrelierten Potentiale (ERPs) ergab, dass die N1-Komponenten, die von Lichtreizen am erstem oder zweiten Ziel ausgelöst wurden, größere Amplituden hatten, als solche, die auf Reize an der irrelevanten Position hin auftraten (siehe Abbildung 3.4). Dies ist direkter physiologischer Beweis dafür, dass beide Zielpositionen einer geplanten Doppelzeigesequenz bei der Handlungsvorbereitung aufgemerkt werden. Dieses Ergebnis replizierte damit die Resultate einer früheren Studie zu Handbewegungssequenzen (Baldauf, Wolf & Deubel, 2006) und lieferte zusätzliche Erkenntnisse über die neuronale Grundlage der beobachteten Aufmerksamkeitsverlagerung. In einem zweiten Experiment dieser Studie (Exp. 2.2) wurde der Frage nachgegangen, ob die beiden Zielpositionen räumlich getrennt von einander selektiert werden (siehe Abbildung 3.6). Dazu wurde das experimentelle Design aus dem vorangegangenen Experiment erweitert. Der irrelevante Dot-probe konnte in Experiment 2.2 auch auf einer Zwischenpositionen erscheinen, die genau zwischen den beiden Zeigezielen plaziert war. Die Analyse der evozierten EEG-Potentiale zeigte, dass die Position zwischen zwei Handlungszielen nicht selektiert wurde (siehe Abbildung 3.7).

Visuelle Aufmerksamkeit vor bimanuellen Bewegungen

In Kapitel 4 der vorliegenden Arbeit beinhaltet eine weitere empirische Studie, welche in drei Experimenten die Rolle der visuellen Aufmerksamkeit vor bimanuellen Zeigebewegungen untersucht. Auch bei bimanuell koordinierten Bewegungen müssen zwei räumlich getrennte Zielpositionen angesteuert werden. Das verwendete Paradigma kombiniert die motorische Aufgabe, bimanuelle Zeigebewegungen auszuführen, mit einer perzeptiven Zweitaufgabe, die es erlaubt zu testen, wo in Sichtfeld visuelle Aufmerksamkeit lag. Abbildung 4.2 zeigt den experimentellen Aufbau und Abbildung 4.2 gibt einen Überblick über den Ablauf der präsentierten Stimuli. Das zentrale Fixationskreuz war umgeben von einer sternförmigen Konfiguration. Zu Beginn eines jeden Trials wurde mit einem zentralen Farb-cue einer der drei farbig umrahmten Balken des Sterns indiziert. Darauf hin mussten die Teilnehmer so schnell und so genau wie möglich mit den zeigefingern der linken und rechten Hand auf die Maskenelemente an den beiden Enden des indizierten Balken zeigen. Während der natürlichen Latenz der Bewegung wurde für 100 ms (SOA=50 ms) an irgendeiner Position ein Zielbuchstabe (′E′ oder ′Ǝ′) und an den übrigen Positionen Distraktoren (′2′ und ′5′) dargeboten. Nach der Präsentation wurden alle Elemente sofort wieder maskiert noch bevor die Bewegung initialisiert wurde. Am Ende jedes Durchgangs musste der Teilnehmer per Tastendruck entscheiden, ob ein ′E′ oder ein ′Ǝ′ präsentiert worden war. Die Analyse der Erkennungsleistungen zeigte, dass es am Ziel der rechten und linken Hand einfacher war, Zielbuchstaben zu erkennen. Außerdem wurde dem weiter entfernten Ziel mehr Aufmerksamkeit zu gewiesen als dem näheren. In einem zweiten Experiment (Exp. 3.2) wurden gleichzeitig zweii Zielbuchstaben präsentiert, die zufällig auf den Zielpositionen liegen konnten, oder aber auf bewegungsirrelevanten Positionen der Anordnung. Ähnlich wie in Experiment 1.3 zeigte sich, dass der Verlgeich nur gelang, wenn beide Zielbuchstaben mit den Handlungszielen zusammenfielen. Die Ergebnisse sprechen dafür, dass beide Zielpositionen parallel aufgemerkt werden. Außerdem scheint die Schwierigkeit eines Ziels (also z.B. seine Distanz vom Augangspunkt bei konstanter Größe des Zieles selbst) zu bestimmen, wie viel Aufmerksamkeit während der motorischen Preparationszeit auf das Ziel verlagert wird. Das letzte Experiment (Exp. 3.3) misst zum Verlgeich die Erkennungsleistungen, wenn nur ein einzelnes Ziel mit nur einer Hand angesteuert wird. In Verbindung mit vorhergehenden Studien (ähnliche Ergebnisse finden sich bei Baldauf, Wolf & Deubel, 2006; Chapman, Gavrilescu, Wang, Kean, Egan, & Castiello, 2002) weisen die Ergebnisse dieses dritten Experiments darauf hin, dass die Gesamtkapazität der visuellen Aufmerksamkeit nicht immer gleich ist, sondern abhängig von den Anforderungen der motorischen Aufgabe variieren kann .

Schlußfolgerungen und Aussichten

Die drei empirischen Studien in Kapitel 2-4 der vorliegenden Arbeit untersuchten die Verlagerung visueller Aufmerksamkeit im Sichtfeld bei der Vorbereitung komplexer Bewegungen. Dabei wurden unterschiedliche Effektorsysteme (Augenbewegungen in Kapitel 2, Handbewegungen in Kapitel 3 und 4) und Handlungen mit unterscheidlicher zeitlicher Anordnung untersucht (sequentielle Handlungen in Kapitel 2 und 3, simultane Ausführung von Bewegungen in Kapitel 4). Ein gemeinsames Charakteristikum aller untersuchten Handlungen war, dass multiple Bewegungsziele vorbereitet werden mussten. Als Gesamtergebnis zeigte sich, dass die Selektion bei der Handlungsplanung ('selection-for-action') alle handlungsrelevanten Zielpositionen umfasst und sich der Focus der Aufmerksamkeit flexibel auf mehrere Zielpositionen aufteilt. Dabei werden zwischenliegende Positionen, die nicht Ziel einer Bewegungskomponente sind, von der bevorzugten visuellen Verarbeitung ausgeschlossen. Mehrere Experimente zeigten, dass es sich hierbei um einen parallelen Selektionsprozess handelt. Besonders für die Vorbereitung von Bewegungssequenzen ist es bemerkenswert, dass die Ziele mehrerer nachfolgenden Bewegungen vorab parallel selektiert werden.

Die vorliegenden Untersuchungen haben aber auch zahlreiche neue Fragestellungen aufgeworfen und inspirieren nachfolgende Studien. Beispielsweise wird weiter untersucht werden, wie die graduelle Zuteilung von attentionalen Gewichten (siehe Exp. 1.1 und 1.2) von der zeitlichen Reihenfolge der vorbereiteten Bewegungskomponenten abhängt. Außerdem ist es interessant zu untersuchen, welche neuronale Population die Selektion multipler Handlungsziele leistet. Weitere Experimente werden auf die Frage fokusieren, unter welchen experimentellen Bedingungen visuelle Aufmerksamkeits in mehrere Foci aufgeteilt wird und wann nicht. Desweiteren könnte es von Interesse sein, ein Modell zu entwickeln, das Vorhersagen treffen kann, wo auf unterschiedlichen Objekten Aufmerksamkeit verlagert wird, wenn diese gegriffen werden sollen. Nicht zu letzt kann eine Folgeuntersuchung dem Teilergebnis in Kapitel 4 nachgehen, dass Ziele, die weiter vom Ausgangspunkt entfernt sind, mehr visuelle Selektion bei der Bewegungsvorbereitung erfahren.

Bibliography

Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review in Neuroscience*, *20*, 303–330.

Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*, *25*, 189–220.

Allport, D. A. (1987). Selection for action: Some behavioral and neurophysiological considerations of attention and action. In H. Heuer & A.F. Sanders (Eds.), *Perspectives on Perception and Action*, 395-419. Hillsdale, NJ: Lawrence Erlbaum Associates.

Averbeck, B.B., Chafee, M.V., Crowe, D.A., & Georgopoulos, A.P. (2002). Parallel processing of serial movements in prefrontal cortex. *Proceedings of the National Academy of Sciences*, 99, 13172-13177.

Averbeck, B.B., & Lee, D. (2007). Prefrontal neural correlates of memory for sequences. *Journal of Neuroscience*, 27(9), 2204-2211.

Awh, E., Armstrong, K.M., & Moore, T. (2006). Visual and oculomotor selection: links, causes and implications for spatial attention. *Trends in Cognitive Sciences*, 10(3), 124.

Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal–directed hand movements. *Vision Research*, 46, 4355–4374.

Baldauf, D., & Deubel, H. (2007). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research,* online URL: http://www.springerlink.com/content/100473.

Baldauf, D., Cui, H., & Andersen, R.A. (2007). The posterior parietal cortex encodes the first and second goal in sequential reaching arm movements. *Annual meeting of the Society for Neuroscience*. Program No. 397.3. San Diego, CA: Online.

Baldauf, D., & Deubel, H. (submitted). Attentional selection of multiple goal positions before rapid hand movement sequences: an ERP study.

Ballard, D.H., Hayhoe, M.M., & Pelz, J.B. (1995). Memory representations in natural tasks. *Journal of Cognitive Neuroscience*, 7(1), 66-80.

Balint, R. (1909). Seelenlähmung des Schauens, optische Apraxie, räumliche Störung der Aufmerksamkeit. *Monatsschriften für Psychiatrische Neurologie*, 25, 51-81.

Batista, A.P., & Andersen, R.A. (2001). The parietal reach region codes the next planned movement in a sequential reach task. *Journal of Neurophysiology*, 85, 539–544.

Batista, A.P., Buneo, C.A., Snyder, L.H., & Andersen, R.A. (1999). Reach plans in eye-centered coordinates. *Science*, 285, 257-260.

Beck, J., & Ambler, B. (1973). The effects of concentrated and distributed attention on peripheral acuity. *Perception & Psychophysics*, 14, 225-230.

Bekkering, H., Pratt, J., & Abrams, R. A. (1996). The gap effect for eye and hand movement. *Perception & Psychophysics, 58*, 628–635.

Bonfiglioni, C., & Castiello, U. (1998). Dissociation of covert and overt spatial attention during prehension movements: selective interference effects. *Perception & Psychophysics*, *60*(8), 1426–1440.

Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature, 226*, 177–178.

Bouma, H. (1973). Visual interference in the parafoveal recognition of initial and final letters of words. *Vision Research, 13*, 767–782.

Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, 97, 523-547.

Bundesen, C., Habekost, T., & Kyllingsbaeck, S. (2005). A neural theory of visual attention: bridging cognition and neurophysiology. *Psychological Review*, 112 (2), 291-328.

Buneo, C.A., Jarvis, M.R., Batista, A.P., & Andersen, R.A. (2002). Direct visuomotor transformations for reaching. *Nature*, 416, 632-636.

Buneo, C., & Andersen, R.A. (2006). The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia*, 44, 2594-2606.

Bushnell, M. C., Goldberg, M. E., & Robinson, D. L. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective attention. *Journal of Neurophysiology*, 46, 755-772.

Calton, J. L., Dickinson, A. R., & Snyder, L. H. (2002). Non-spatial, motorspeciWc activation in posterior parietal cortex. *Nature Neuroscience*, 5, 580–588.

Carrasco M, Penpeci–Talgar, C, & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Research*, 40, 1203–15.

Castiello, U., & Umilta, C. (1990). Size of the attentional focus and efficiency of processing. *Acta Psychologica*, 73, 195-209.

Castiello,U., & Umilta, C. (1992). Splitting focal attention. *Journal of Experimental Psychology: Human Perception & Performance*, 18, 837-848.

Castiello, U., & Bennett, K.M.B. (1997). The bilateral reach-to-grasp movement of Parkinson desease subjects. *Brain*, 129, 593-604.

Castiello, U., Bennett, K.M.B., & Stelmach, G.E. (1997). The bilateral reach-to-grasp movement. *Behavioural and Brain Research*, 56, 43-557.

Castiello, U. (1996). Grasping a fruit: Selection for action. *Journal of Experimental Psychology: Human Perception & Performance*, 22, 582–603.

Cavanagh, P. (2004). Attention routines and the architecture of attention. In: M. Posner (Ed.), *Cognitive Neuroscience of Attention*. New York: The Guilford Press, pp. 13-28.

Cavanaugh, J., & Wurtz, R.H. (2004). Subcortical modulation of attention counters change blindness. *Journal of Neuroscience*, 24(50), 11236–11243.

Chelazzi, L., & Corbetta, M. (2000). Cortical mechanisms of visuospatial attention in the primate brain. In M. S. Gazzaniga (Ed.). *The New Cognitive Neuroscience* (pp. 667–686). Cambridge, MA: MIT Press.

Chapman, H., Gavrilescu, M., Wang, H., Kean, M., Egan, K., & Castiello, U. (2002). Posterior parietal cortex control of reach-to-grasp movements in humans. *European Journal of Neuroscience*, 15, 2037 - 2042.

Colby, C. L. (1998). Action-oriented spatial reference frames in cortex. *Neuron*, 20, 15–24.

Colby, C. L., Duhamel, J. R., & Goldberg, M. E. (1996). Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. *Journal of Neurophysiology*, 76, 2841-2852.

Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual review of Neuroscience*, 22, 319–349.

Corbetta, M., Miezin, F., Shulman, G., & Peterson, S. (1991). Selective and divided attention during visual discriminations of shape, color and speed: Functional anatomy by positron emission tomography. *Journal of Neuroscience*, 11, 2383–2402.

Corbetta, M., Shulman, G. L., Miezin, F. & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, 270, 802-805.

Corbetta, M., Shulman, G.L., Conturo, T.E., Snyder, A.Z., Akbudak, E., Petersen, S.E., & Raichle, M.E. (1997). Functional magnetic resonance imaging (fMRI) of visuospatial attention: group and single subject analysis. *Neuroimage*, 5, 85.

Corbetta, M., & Shulman, G.L. (1998). Human cortical mechanisms of visual attention during orienting and search. *Philosophical Transactions of the Royal Society of London*, 353, 1353-1362.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, *3*, 292–297.

Corbetta, M., & Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Review Neuroscience*, 3, 201-215.

Craighero, L., Fadiga, L., Rizzolatti, G., & Umilta, C. (1998). Visuomotor priming. *Visual Cognition*, *5*, 109-125.

Christ, R.E., Li, W., & Gilbert, C.D. (2001). Learning to see: experience and attention in primary visual cortex. *Nature Neuroscience*, 4, 519-525.

Cui, H., & Andersen, R.A. (2007). Posterior parietal cortex encodes autonomously selected motor plans during effector choice. *Annual meeting of the Society for Neuroscience*. Program No. 507.5. San Diego, CA: Online.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition – Evidence for a common attentional mechanism. *Vision Research*, *36*, 1827-1837.

Deubel, H., Schneider, W.X., & Paprotta, I. (1996). Visual attention and manual aiming: Evidence for obligatory and selective spatial coupling. *Perception*, 25, 13-14.

Deubel, H., Shimojo, S., & Paprotta, I. (1997). The preparation of goal-directed movements requires selective attention: Evidence from the line-motion illusion. *Perception*, *26*, 72.

Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: Evidence for a common attentional mechanism in reaching and perception. *Visual Cognition*, *5*, 81-107.

Deubel, H., & Schneider, W.X. (2003). Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. *Annals of the New York Academy of Sciences*, 1004, 289–296.

Deubel, H., & Schneider, W. X. (2004). Attentional selection in sequential manual movements, movements aroand an obstacle and in grasping. In Humphreys, G. W. & Riddoch, M. J. (Eds.), *Attention in Action*. Hove: Psychology Press.

DeRenzi, E. (1982). Disorders of space exploration and cognition. New York:Wiley.

Desimone, R., Moran, J., & Spitzer, H. (1989). Neural mechanisms of attention in extrastriate cortex of monkeys. In M. Arbib & S. Amari (Eds.): *Dynamic inter- actions in neural networks: models and data*, pp. 169-182. NewYork: Springer.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193-222.

Diedrichsen, J., Hazeltine, E., Kennerley, S., & Ivry, R.B. (2001). Moving to directly cued locations abolishes spatial interference during bimanual actions. *Psychological Science*, 12(6), 493-8.

Diedrichsen, J., Ivry, R.B, Hazeltine, E., Kennerley, S., & Cohen, A. (2003). Bimanual interference associated with the selection of target locations. *Journal of Experimental Psychology: Human Perception & Performance*, 29(1), 64-77.

Droll, J. A., Hayhoe, M. M., Triesch, J., & Sullivan, B. T. (2005). Task demands control acquisition and storage of visual information. *Journal of Experimental Psychology: Human Perception & Performance*, 31, 1416-1438.

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, 113, 501-517.

Duncan, J., Ward, R., & Shapiro, K. (1994). Direct measurement of attentional dwell time in human vision. *Nature*, 369, 313-315.

Eason, R.G. (1981). Visual evoked potential correlates of early neural filtering during selective attention. *Bulletin of the Psychonomic Society*, 18, 203-206.

Egly, R., & Homa, D. (1984). Sensitization of the visual field. *Journal of Experimental Psychology: Human Perception & Performance*, 10, 778-793.

Eimer, M., Van Velzen, J., & Driver, J. (2002). Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, 14, 254-271.

Eimer, M., Van Velzen, J., Forster, B., & Driver, J. (2003). Shifts of attention in light and in darkness: An ERP study in supramodal attentional control and crossmodal links in spatial attention. *Cognitive Brain Research*, 15, 308-323.

Eimer, M., Forster, B., Van Velzen, J., & Prabhu, G. (2005). Covert manual response preparation triggers attentional shifts: ERP evidence for the premotor theory of attention. *Neuropsychologia*, 43, 957-966.

Eimer, M., Van Velzen, J., Gherri, E., & Press, C. (2006). Manual response preparation and saccade programming are linked to attention shifts: ERP evidence for covert attentional orienting and spatially specific modulations of visual processing. *Brain Research*, 1105(1), 7-19.

Eriksen, C.W., & Hoffman, J.E. (1972). Temporal and spatial characteristics of selective encoding from visual displays. *Perception & Psychophysics*, 12, 201-204.

Eriksen, C.W., & Yeh, Y.Y. (1985). Allocation of attention in the visual field. *Journal of Experimental Psychology: Human Perception & Performance*, *11*, 583–597.

Eriksen, C.W., & St. James, J.D. (1986). Visual attention within and aroand focal attention: A zoom lens model. *Perception & Psychophysics*, *40*(4), 225–240.

Festinger, L. (1983). The human legacy. New York: Columbia University Press, pp. 3-12.

Findlay, J.M., & Gilchrist, I.D. (2005). Active vision: the psychology of looking and seeing. Oxford: University Press.

Fischer, B., & Weber, H. (1993). Express saccades and visual attention. *Behavioral Brain Science 16*, 588–589.

Fitts, P.M. (1954). The information capacity in the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, 47(6), 381-391.

Fitts, P.M., & Peterson, J.R. (1964). Information capacity of discrete motor responses. *Journal of Experimental Psychology*, 67(2), 103-112.

Franz, E.A., Zelaznik, H.N., & McCabe, G. (1991). Spatial topological constraints in a bimanual task. *Acta Psychologica*, 77, 137–151.

Franz, E.A., Eliassen, J.C., Ivry, R.B., & Gazzaniga, M.S. (1996). Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. *Psychological Science*, 7, 306–310.

Fuji, N., & Graybiel, A.M. (2003). Representation of action sequence boundaries by macaque prefrontal cortical neurons. *Science*, 301, 1246-1249.

Gersch, T. M., Kowler, E., & Dosher, B. (2004). Dynamic allocation of visual attention during the execution of sequences of saccades. *Vision Research*, *44*, 1469–1483.

Godijn, R., & Theeuwes, J. (2003). Parallel Allocation of Attention Prior to the Execution of Saccade Sequences. *Journal of Experimental Psychology: Human Perception & Performance*, *29*(5), 882–896.

Gratton, G., Coles, M.G.H., & Donchin, E. (1983) A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55, 468-484.

Graziano, M.S.A., & Gross, C.G. (1994). Mapping space with neurons. *Current Directions in Psychological Science*, *3*, 164-167.

Green, J.J., Teder-Salejarvi, W.A., & McDonald, J.J. (2005). Control mechanisms mediating shifts of attention in auditory and visual space: a spatio-temporal ERP analysis. *Experimental Brain Research*, 166, 358-369.

Hahn, S., & Kramer, A.F. (1998). Further evidence for the division of attention among non-contiguous locations. *Visual Cognition*, *5*, 217–256.

Halsband, U., Matsuzaka, Y., & Tanji, J. (1994). Neural activity in the primate supplementary, pre-supplementary and premotor cortex during externally and internally instructed sequential movvements. *Neuroscience Research*, *20*, 149–155.

Hawkins, H. L., Hillyard, S. A., Luck, S. J., Mouloua, M., Downing, C. J. & Woodward, D. P. (1990). Visual attention modulates signal detectability. *Journal of Experimental Psychology: Human Perception & Performance*, 16, 802-811.

Hayhoe, M., Land, M., & Shrivastava, A. (1999). Coordination of eye and hand movements in a normal environment. *Investigative Ophthalmology and Vision Science*, 40, 380.

Hayhoe, M., Shrivastava, A., Mruczek, R., & Pelz, J.B. (2003). Visual memory and motor planning in natural tasks. *Journal of Vision*, 3 (1), 49-63.

Heilman, K.M., Watson, R.T., & Valenstein, E. (1985). Neglect and related disorders. In K. M. Heilman & E. Valenstein (Eds.): *Clinical neuropsychology*, pp. 243-293. New York: Oxford University Press.

Heinze, H.J., Luck, S.J., Munte, T.F., Gös, A., Mangun, G.R., & Hillyard, S.A. (1994). Attention to adjacent and seperate positions in space: an electrophysiological analysis. *Perception & Psychophysics*, 56 (1), 42-52.

Heinze, H. J. et al. (1994). Combined spatial & temporal imaging of brain activity during visual selective attention in humans. *Nature*, 372, 543-546.

Henderson, J. M. (1996). Spatial precues a¡ect target discrimination in the absence of visual noise. *Journal of Experimental Psychology: Human Perception & Performance*, 22, 780-787.

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1993). Focal visual attention produces illusiory temporal order and motion sensation. *Vision Research*, *33*, 1219–1240.

Hillyard, S.A., & Munte, T.F. (1984). Selective attention to colour and location: An analysis with event-related brain potentials. *Perception & Psychophysics*, 36, 185-198.

Histed, M.H., & Miller, E.K. (2006). Microstimulation of frontal cortex can reorder a remembered spatial sequence. *PLoS Biology*, 4 (5), 134.

Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, *57*, 787-795.

Hopf, J.M., & Mangun, G.R. (2000). Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, 111, 1241-1257.

Howard, L.A., & Tipper, S.P. (1997). Hand deviations away from visual cues: indirect evidence for inhibition. *Experimental Brain Research*, 113, 144–152.

Humphreys, G.W., Riddoch, M.J., Linnell, K.J., Punt, D.J., Edwards, M.G., & Wing, A.M. (2005). Attending to what you are doing. Neurophysiological and experimental evidence for interactions between perception and action. In G.W. Humphreys & M.J. Riddoch: *Attention in Action. Advances from Cognitive Neuroscience.* Psychology Press, New York.

Ihaka R., & Gentleman, R. (1996). R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, 5, 299–314.

Intriligator, J., & Cavanagh, P. (2001). The Spatial Resolution of Visual Attention. *Cognitive Psychology, 43*, 171–216.

Irwin, D.E., & Gordon, R.D. (1998). Eye movements, attention, and transsaccadic memory. *Visual Cognition*, 5,127-155.

Ito, M., & Gilbert, C.D. (1999). Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron*, 22, 593-604.

Jackson, S.R., Jackson, G.M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Experimental Brain Research*, 102, 519–530

Jackson, G.M., German, K., & Peacock, K. (2002). Functional coupling between the limbs during bimanual reach-to-grasp movements. *Human Movement Sciences*, 21(3), 317-333.

Jackson, G.M., Jackson, S.R., & Kritikos, A. (1999). Attention for action: Coordinating bimanual reach-to-grasp movements. *British Journal of Psychology*, 90, 247-270.

James, W. (1890). The principals of psychology. New York: Oxford University Press.

Jeannerod, M. (1994). The representing brain: neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, 17, 187–245.

Johansson, R.S., Westling, G., Bäckström, A., & Flanagan, J.R. (2001). Eye-hand coordination in object manipulation. *Journal of Neuroscience*, 21, 6917–6932.

Johnson, P. B., Ferraina, S., Bianchi, L., & Caminiti, R. (1996). Cortical networks for visual reaching: physiological and anatomical organization of frontal and parietal arm regions. *Cerebral Cortex*, 6, 102–119.

Jovancevic, J., B. Sullivan, et al. (2006). Control of attention and gaze in complex environments. *Journal of Vision*, 6(12), 1431-50.

Kahneman, D. (1973). Attention and effort. Englewood Cliffs, NJ: Prentice-Hall.

Kanvisher, N., & Wojciulik, E. (2000). Visual attention: insights from brain imaging. *Nature Neuroscience Review*, 1, 91-100.

Kapstein, N.A., Theeuwes, J., & Van der Heijden, A.H.C. (1995).Search for a conjunctively defined target can be selectively limited to a color defined subset of elements. *Journal of Experimental Psychology: Human Perception & Performance*, 21, 1053-1069.

Karnath, H.O. (1988). Deficits of attention in acute & recovered visual hemi-neglect. *Neuropsychologia*, 26, 27 -43.

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L.G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron, 22*, 751–761.

Kawashima, R., Naitoh, E., Matsumura, M., Itoh, H., Ono, S., & Satoh, K. (1996). Topographic representation in human intraparietal sulcus of reaching and saccade. *Neuroreport*, 7, 1253–1256.

Keele, S.W. (1986). Motor control. In K.R. Boff, L. Kaufman & J.P. Thomas (Eds.), *Handbook of perception & performance*, Vol. II. New York: Wiley.

Kelso, J.A.S., Putnam, C.A., & Goodman, D. (1983). On the space-time structure of human interlimb coordination. *Quaterly Journal of Experimental Psychology*, 35, 347-375.

Kelso, J.A.S., Southard, D.L., & Goodman, D. (1979a). On the nature of human interlimb coordination. *Science*, 203, 1029–1031.

Kelso, J.A.S., Southard, D.L., & Goodman, D. (1979b). On the coordination of two-handed movements. *Journal of Experimental Psychology*, 5, 229–238.

Kelso, J.A.S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. MIT Press, Cambridge, MA.

Kettner, R.E., Marcario, J.K., & Port, N.I. (1996). Control of remembered reaching sequences in monkey. II. Storage and preparation before movement in motor and premotor cortex. *Experimental Brain Research*, 112, 317–358.

Konen, C. S., Kleiser, R., Wittsack, H. J., Bremmer, F., & Seitz, R. J. (2004). The encoding of saccadic eye movements within human posterior parietal cortex. *Neuroimage*, *22*, 304–314.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*, 1897-1916.

Kramer, A. F., & Hahn, S. (1995). Splitting the beam: Distribution of attention over noncontiguous regions of the visual field. *Psychological Science*, *6*, 381–386.

Kritikos, A., Bennett, K. M. B., Dunai, J., & Castiello, U. (2000). Interference from distractors in reach-to-grasp movements. *Quarterly Journal of Experimental Psychology*, *53*, 131–151.

Kroese, B., & Julesz, B. (1989). The control and speed of shifts in attention. *Vision Research*, *29*, 1607–1619.

LaBerge, D., & Brown, V. (1989). Theory of attentional operations in shape identification. *Psychological Review*, *96*(1), 101–124.

Land, M. F., & Lee, D. N. (1994). Where we look when we steer. *Nature*, 369, 742-744.

Land, M. F. (1998). The visual control of steering. In L. R. Harris & K. Jenkin (Eds.): *Vision and action*. Cambridge, UK: Cambridge University Press, pp. 163-180.

Land, M.F, Mennie, N, & Rusted, J. (1999). Eye movements and the roles of vision in activities of daily living: making a cup of tea. *Perception*, 28, 1311–1328.

Lee, T.D., Almeida, Q.J., & Chua, R. (2002) Spatial constraints in bimanual coordination: influences of effector orientation. *Experimental Brain Research*, 146, 205–212.

Li, W., Piech, V., & Gilbert, C.D. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, 7(6), 651-655.

Logan, G. D. (2005). The time it takes to switch attention. *Psychonomic Bulletin & Review*, 12 (4), 647–653.

Lu, J., & Itti, L. (2005). Perceptual consequences of feature-based attention. *Journal of Vision*, 5, 622-631.

Luck, S.J. (2005). An Introduction to the event-related potential technique. Cambridge, Massachusetts: MIT Press.

Luck, S. J., & Hillyard, S.A. (1995). The role of attention in feature detection and conjunction discrimination: An electrophysiological analysis. *International Journal of Neuroscience*, 80, 281-297.

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception & Performance*, 20, 887-904.

Mackeben, M., & Nakayama, K. (1993). Express attentional shifts. *Vision Research*, *33*(1), 85–90.

Matelli, M., Govoni, P., Galetti, C., Kutz, D. F., & Luppino, G. (1998). Superior area 6 afferents from the superior parietal lobule on the macaque monkey. *Journal of Comparative Neurology*, 402, 327–352.

Madden, D. (1992). Selective attention and visual search: Revision of an allocation model and application to age differences. *Journal of Experimental Psychology: Human Perception & Psychophysics, 18*, 821–836.

Mangun, G.R., & Hillyard, S.A. (1987). The spatial allocation of visual attention as indexed by event-related brain potentials. *Human Factors*, 29(2), 195-211.

Mangun, G.R., & Hillyard, S.A. (1988). Spatial gradients of visual attention: Behavioural and electrophysiological evidence. *Electroencephalography and Clinical Neurophysiology*, 70, 417-428.

Mangun, G.R., & Hillyard, S.A. (1990). Allocation of visual attention to spatial locations. Trade-off functions of event-related brain potentials and detection performance. *Perception & Psychophysics*, 47, 532-550.

Mangun, G.R., & Hillyard, S.A. (1991). Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception & Performance*, 17, 1057-1074.

Mangun, G.R., Hillyard, S.A., & Luck, S. (1993). Electrocortical substrates of visual selective attention. In D. Meyer & S. Kornblum: *Attention and Performance XIV*, Cambridge, MA, MIT-Press, 219-243.

Mangun, G.R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*, 32, 4-18.

McAdams, C. J. & Maunsell, J. H. R. (1997). Spatial attention and feature-directed attention can both modulate responses in macaque areaV4. *Society for Neuroscience*, Abstract 23, 2062.

Mennie, N., Hayhoe, M., & Sullivan, B. (2007). Look-ahead fixations: anticipatory eye movements in natural tasks. *Experimental Brain Research*, 179(3), 427-442.

Mesulam, M.-M. (1990). Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Annual Neurology*, 28, 597-613.

Mazzoni P., Bracewell, R.M., Barash, S., & Andersen, R.A. (1996). Motor intention activity in the macaque's lateral intraparietal area. I. Dissociation of motor plan from sensory memory. *Journal of Neurophysiology*, 76 (3), 1439–1456.

Medendorp, W.P., Goltz, H.C., & Vilis, T. (2006). Directional selectivity of BOLD activity in human posterior parietal cortex for memory–guided double–step saccades. *Journal of Neurophysiology*, 95, 1645–1655.

Melcher, D., Papathomas, T.V., & Vidnyanszky, Z. (2005). Implicit attentional selection of bound features. *Neuron*, 46, 723-729.

Michie, J.P., Bearpark, H.M., Crawford, J.M., & Glue, L.C.T (1987). The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology*, 24, 449-463.

Moore, C. M., Egeth, H., Berglan, L. R., & Luck, S. J. (1996). Are attentional dwell times inconsistent with serial visual search? *Psychonomic Bulletin & Review*, 3, 360-365.

Moore, C.M., & Egeth, H. (1998). How does feature-based attention affect visual processing? *Journal Experimental Psychology: Human Perception & Performance*, 4, 1296-1310.

Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, 91, 152–162.

Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Science*, 98(3), 1273–1276.

Moore, T., & Armstrong, K.M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, 421, 370.

Moran, J. & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, 229, 782-784.

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli. *Journal of Neurophysiology*, 70, 909-919.

Motter, B. C. (1994). Neural correlates of attentive selection for color or luminance in extrastriate area V4. *Journal of Neuroscience*, 14, 2178-2189.

Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H., & Acuna, C. (1975). Posterior parietal cortex of the monkey: command functions for operation within extrapersonal space. *Journal of Neurophysiology*, 38, 871–908

Müller, H.J., & Rabbitt, P.M (1989). Spatial cueing and the relation between the accuracy of 'where' and 'what' decisions in visual search. *Quaterly Journal of Experimental Psychology*, 41(4), 747-73.

Müller, M.M., & Hübner, R. (2002). Can the spotlight of attention be shaped like a doughnut? Evidence from steady-state visual evoked potentials. *Psychological Science*, 13(2),119-24

Müller, M.M., Teder-Salejarvi, W., & Hillyard, S.A. (1998). The time course of cortical facilitation during cued shifts of spatial attention. *Nature Neuroscience*, 1, 631-634.

Müller, M.M., Malinowski, P., Gruber, T., & Hillyard, S.A. (2003). Sustained division of the attentional spotlight. *Nature*, 424, 309-312.

Mulliken, G., & Andersen, R.A. (2006). Online dírectional control signals in posterior parietal cortex. *Annual meeting of the Society for Neuroscience*. Program No. 242.21. Atlanta, GA: Online.

Mushiake, H. Saito, N., Sakamoto, K. Itoyama, Y., & Tanji, J. (2006). Activity in the lateral prefrontal cortex reflects multiple steps of future events in action plans. *Neuron*, 50, 631–641.

Neisser, U. (1967). Cognitive psychology. NewYork: Appleton-Century-Crofts.

Neumann, O. (1987). Beyond capacity: A functional view of attention. In H. Heuer & A.F. Sanders (Eds.), *Perspectives on Perception and Action*, 361-394. Hillsdale, NJ: Lawrence Erlbaum Associates.

Ninokura, Y., Mushiake, H., & Tanji, J. (2003). Representation of the temporal order of visual objects in the primate lateral prefrontal cortex. *Journal of Neurophysioloy*, 89(5), 2868-2873.

Ninokura, Y., Mushiake, H., & Tanji, J. (2004). Integration of temporal order and object information in the monkey lateral prefrontal cortex. *Journal of Neurophysioloy*, 91(1), 555-560.

Nobre, A.C., Sebestyen, G.N., Gitelman, D.R., Mesulam, M.M., Frackowiack, R.S.J., & Frith, C.D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, 120, 515-533.

Nobre, A.C., Sebestyen, G.N., & Miniussi, M. (2000). The dynamics of shifting visuospatial attention revealed by event-related potentials. *Neuropsychologia*, 38(7), 964-74.

Ohbayashi, M., Ohki, K., & Miyashita, Y. (2003). Conversion of working memory to motor sequences in the monkey premotor cortex. *Science*, 301, 233-236.

O'Connor, D.H., Fukui, M.M., Pinsk, M.A., & Kastner, S. (2003). Attention modulates responses in the human lateral geniculate nucleus. *Nature Neuroscience*, 5(11), 1203-1209.

Paprotta, I., Deubel, H., & Schneider, W.X. (1999). Object recognition and goal-directed eye or hand movements are coupled by visual attention. In W. Becker, H. Deubel & T. Megner (Eds.): *Current Oculomotor Research: Physiological and Psychological Aspects*, 241-248. New York, London: Plenum.

Pelz, J.B., & Canosa, R. (2001). The coordination of eye, head, and hand movements in a natural task. *Experimental Brain Research*, 139 (3), 266-277.

Pernier, J., Perrin, F., & Bertrand, O. (1988). Scalp current densitiy fields: Concept and properties. *Electroencephalography and Clinical Neurophysiology*, 9, 45-479.

Pesaran, B., Nelson, M. J., & Andersen, R. A. (2006). Dorsal premotor neurons encode the relative position of the hand, eye and goal during reach planning. *Neuron*, 51 (1), 125-134.

Pesaran, B., Nelson, M., & Andersen, R.A. (submitted). Free choice increases neuronal interactions between frontal and parietal cortex.

Pestillo, F., & Carrasco, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Research*, 45, 1867-1875.

Podgorny, P., & Shepard, R.N. (1983). Distribution of attention over space. *Journal of Experimental Psychology. Human Perception & Performance*, 9, 380-393.

Posner, M.I. (1978). Chronometric exploration of mind. Hillsdale, NJ: Lawrence Erlbaum Associates.

Posner, M.I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3-25.

Remington, R. W. (1980). Attention and saccadic eye movements. *Journal of Experimental Psychology: Human Perception & Performance*, 6(4), 726-44.

Riddoch, M.J., Humphreys, G.W., Edwards, S., Baker, T., & Wilson, K. (2003). Actions glue objects but associations glue words: neuropsychological evidence for multiple object selection. *Nature Neuroscience*, 6, 82-89.

Riek, S., Tresilian, J.R., Mon-Williams, M., Coppard, V.L., & Carson, R. G. (2003). Bimanual aiming and overt attention: one law for two hands. *Experimental Brain Research*, 153(1), 59-75.

Rizzolatti, G., Riggio, L., & Sheliga, B.M. (1994). Space and selective attention. In C. Umilta & M. Moscovitch (Eds.), *Attention and Performance XV. Conscious and Non-conscious Information Processing*, 231-265. Cambridge, MA: MIT Press.

Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favour of a premotor theory of attention. *Neuropsychologia*, 25, 31-40.

Robinson, D.L., Bowman, E.M., & Kertzman, C. (1995). Covert orienting of attention in macaques. II. Contributions of parietal cortex. *Journal of Neurophysiology*, 74, 698-721.

Roelfsema, P.R., Lamme, V.A., & Spekreljse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature*, 395, 376-381.

Rosenbaum, D.A. (1980). Human movement initiation: Specification of arm, direction, and extent. *Journal of Experimental Psychology: General*, 109, 444–474.

Rosenbaum, D.A., & Kornblum, S. (1982). A priming method for investigating the selection of motor responses. *Acta Psychologica*, 51, 223–243.

Saenz, M., Buracas, G.T., & Boynton, G.M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, 5, 631-632.

Saenz, M., Buracas, G.T., & Boynton, G.M. (2003). Global feature-based attention for motion and color. *Vision Research*, 43, 629-637.

Sagi, D., & Julesz, B. (1986). Enhanced detection in the aperture of focal attention during simple discrimination tasks. *Nature*, 321, 69345.

Sato, T.R., & Schall, J.D. (2003). Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron*, 38, 637–648.

Scherberger, H., & Andersen, R.A. (2007). Target selection signals for arm reaching in the posterior parietal cortex. *Journal of Neuroscience*, 27(7), 415-125.

Schiegg, A., Deubel, H., & Schneider, W.X. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition*. 10(4), 409.

Schneider, W. X. (1995). VAM: A neuro-cognitive model for attention control of segmentation, object recognition and space-based motor action. *Visual Cognition*, *2*, 331–374.

Schneider, W.X., & Deubel, H. (2002). Selection-for-perception and selection-for-spatialmotor-action are coupled by visual attention: a review of recent findings and new evidence from stimulus-driven saccade control. In W. Prinz & B. Hommel (Eds.), *Attention and Performance XIX: Common Mechanisms in Perception and Action*, 609–627. Oxford: Oxford University Press.

Schöner, G., & Kelso, J.A.S. (1988). Dynamic pattern generation in behavioral and neural systems. *Science*, 239, 1513–1520.

Shaw, M.L. (1978). A capacity allocation model for reaction time. *Journal of Experimental Psychology: Human Perception & Performance*, 4, 586-598.

Shaw, M.L., & Shaw, P. (I977). Optimal allocation of cognitive resources to spatial locations. *Journal of Experimental Psychology: Human Perception & Performance*, 3, 201-211.

Sheliga, B.M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, 98, 507-522.

Shepherd, M., Findlay, J.M., et al. (1986). The relationship between eye movements and spatial attention. *Quaterly Journal of Experimental Psychology*, 38(3), 475-91.

Shima, K., & Tanji, J. (2000). Neuronal activity in the supplementary and pre-supplementary areas for temporal organization of multiple movements. *Journal of Neurophysiology*, 84, 2148-2160.

Shulman, G. L., Remington, R.W. et al. (1979). Moving attention through visual space. *Journal of Experimental Psychology: Human Perception & Performance*, 5(3), 522-6.

Slagter, H.A., Kok, A., Mol, N., & Kenemans, J.L. (2005). Spatio-temporal dynamics of top-down control: directing attention to locaiton and/or color as revealed by ERPs and source modeling. *Cognitive Brain Research*, 22, 333-348.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature*, *386*, 167–170.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (2000). Intention-related activity in the posterior parietal cortex. *Vision Research*, *40*, 1433-1441.

Spijkers, W., & Heuer, H. (1995). Structural constraints on the performance of symmetrical bimanual movements with different amplitudes. *Quarterly Journal of Experimental Psychology*, 48A, 716–740.

Spijkers, W., Heuer, H., Kleinsorge, T., & van der Loo, H. (1997). Preparation of bimanual movements with same and different amplitudes: Specification interference as revealed by reaction time. *Acta Psychologica*, 96, 207–227.

Spijkers, W., Heuer, H., Steglich, C., & Kleinsorge, T. (2000). Specification of movement amplitudes for the left and right hands: Evidence for transient parametric coupling from overlapping-task performance. *Journal of Experimental Psychology: Human Perception & Performance*, 26, 1091–1105.

Steinmetz, M. A. & Constantinidis, C. (1995). Neurophysiological evidence for a role of posterior parietal cortex in redirecting visual attention. *Cerebral Cortex*, 5, 448-456.

Swinnen, S.P., Dounskaia, N., Levin, O., & Duysens, J. (2001). Constraints during bimanual coordination: the role of direction in relation to amplitude and force requirements. *Behavioural Brain Research*, 123, 201–218.

Tanji, J., & Shima, K. (1994). Role for supplementary motor area cells in planning several movements ahead. *Nature*, 371, 413-416.

Theeuwes, J., Godijn, R., & Pratt, J.(2004). A new estimation of the duration of attentional dwell time. *Psychonomic Bulletin & Review*, 11 (1), 60-64

Thompson, K.G., Biscoe, K.L., & Sato, T.R. (2005). Neuronal Basis of Covert Spatial Attention in the Frontal Eye Field. *Journal of Neuroscience*, 25(41), 9479 –9487.

Tipper, S.P., Brehaut, J.C., & Driver, J. (1990). Selection of moving and static objects for the control of spacially based attention. *Journal of Experimental Psychology: Human Perception & Performance*, *16*, 492–504.

Tipper, S. P., Lortie, C., & Baylis, G. C. (1992). Selective reaching: Evidence for action centered attention. *Journal of Experimental Psychology: Human Perception & Performance*, *18*, 891–905.

Tipper, S.P., Weaver, B., Jerreat, L.M., & Burak, A.L. (1994). Object–based and environment–based inhibition of return of visual attention. *Journal of Experimental Psychology: Human Perception & Performance*. *20*, 478–499.

Tipper, S.P., Howard, L.A., & Jackson, S.R. (1997). Selective reaching to grasp: Evidence for distractor interference effects. *Visual Cognition*, 4, 1-38.

Tipper, S.P., Howard, L.A., & Houghton, G. (1998). Action-based mechanisms of attention. *Philosophical Transition of the Royal Society of London*, B 353, 1385–1393.

Titchener, E. M. (1908). *Lectures on the elementary psychology of feeling and attention*. New York: Macmillan.

Treisman, A., & Gelade, G. (1980). A feature–integration theory of attention. *Cognitive Psychology*. *12*(1), 97–136.

Treue, S., & Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature*, 382, 539-541.

Triesch, J., Ballard, D. H., Hayhoe, M. M., & Sullivan, B. T. (2003). What you see is what you need. *Journal of Vision*, 3(1), 86-94.

Tsal, Y. (1983). Movements of attention across the visual field. *Journal of Experimental Psychology. Human Perception & Performance*, 4, 523-530.

Ullman, S. (1984). Visual routines. *Cognition*, 18, 97-157.

Vandenberghe, R., Duncan, J., Dupont, P., Ward, R., Poline, J.-B., Bormans, G., Michiels, J., Mortelmans, L., & Orban, G. A. (1997). Attention to one or two features in left and right visual field: a positron emission tomography study. *Journal of Neuroscience*, 17, 3739-3750.

Vandenberghe, R., Dupont, P., Debruyn, B., Bormans, G., Michiels, J., Mortelmans, L., & Orban, G. A. (1996). The in£uence of stimulus location on the brain activation pattern in detection and orientation discriminationöa PET study of visual attention. *Brain*, 119, 1263-1276.

Van der Lubbe, R.H.J., Wauschkuhn, B., Wascher, E., Niehoff, T., Kömpf, D., & Verleger, R. (2000). Lateralized EEG components with direction information for the preparation of saccades versus finger movements. *Experimental Brain Research*, 132, 163-178.

VanRullen, R., Carlson, T., & Cavanagh, P. (2007). Dividing attention between multiple targets: simultaneous or sequential allocation? *Journal of Vision*, 7(9), p. 642

Van der Stigchel, S., & Theeuwes, J. (2005). The influence of attending to multiple locations on eye movements. *Vision Research*, 45(15), 1921-1927.

Wallis, G., & Bülthoff, H. (2000). What is scene and not seen: Influences of movement and task upon what we see. *Visual Cognition*, 7, 175-190.

Wardak, C., Ibos, G., Duhamel, J., & Olivier, E. (2006). Contribution of the monkey frontal eye field to covert visual attention. *Journal of Neuroscience*, 26(16), 4228–4235.

Ward, R., Duncan, J., & Shapiro, K. (1996). The slow time course of visual attention. *Cognitive Psychology, 30*, 79–109.

Ward, R., Duncan, J., & Shapiro, K. (1997). Effects of similarity, difficulty, and nontarget presentation on the time course of visual attention. *Perception & Psychophysics*, 59, 593-600.

Wardak, C., Ibos, G., Duhamel, J.R., & Olivier, E. (2006). Contribution of the monkey frontal eye field to covert visual attention. *Journal of Neuroscience*, 26(16), 4228–4235.

Wiesendanger, M. (1999). Manual dexterity and the making of tools – an introduction from an evolutionary perspective. *Experimental Brain Research*, 128, 1-5.

Woldroff, M., Fox, T., Matzke, M., Veeraswamy, S., Jerabek, P., & Martin, C. (1995). Combined PET and REP study of sustained visual spatial attention and visual target detection. *Human Brain Mapping*, 1, 49.

Wolf, W., & Deubel, H. (1997). P31 phosphor persistence at phototopic luminance level. *Spatial Vision*, 4, 323–333.

Yarbus, A. L. (1967). Eye movements & vision. New York, NY: Plenum Press.

List of Figures

List of Tables

Curriculum Vitae

1979	born 25th of March in Munich
1998	Abitur (Wittelsbacher-Gymnasium, Munich)
1998 -1999	Civilian service, Ebersberg
1999 - 2000	Study at the Academy of Plastic Arts, Munich
2000 - 2005	Study of Psychology and Neurobiology at the Ludwig-Maximilians-University, Munich
2005	Diploma in Psychology, Ludwig-Maximilians-University, Munich
2005 -2007	PhD-studies in the Graduate School 'Orientation and Motion in Space' (GRK 1091), Ludwig-Maximilians-University, Munich
2006 -2007	Research at the California Institute of Technology, Pasadena, CA (U.S.A.)