

Properties of attentional selection during the preparation of sequential saccades

Daniel Baldauf · Heiner Deubel

Received: 5 April 2007 / Accepted: 17 August 2007 / Printed: 2008
© Springer-Verlag 2008

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 “3”) 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.

Keywords Visual attention · Movement sequences · Eye movements · Selection-for-action · Movement preparation · Saccades · Saccade sequences

Introduction

In order to use its limited capacity in an optimal manner, the visual system processes only certain parts of the visual scene to such a degree as to encode this information in visual short-term memory, and to make it usable for guiding actions. Visual attention serves as a filter mechanism for this selective processing. Thus, attention leads to a prioritized perception of certain parts or aspects of the visual layout in that it facilitates the detection of certain stimuli (e.g., Posner 1980; Carrasco et al. 2000), enables integration of the features that belong to an object (Treisman and Gelade 1980), and determines which objects will be stored in visual short-term memory. This first function of visual attention has been termed “selection-for-perception” (Allport 1987). On the other hand, visual attention is also involved in the selection of objects that are relevant for goal-directed actions. Here, it is assumed that attention provides the relevant spatial information about the targets for intended movements of the motor system and helps to specify the spatial parameters of the movement (Neumann 1987). Allport (1987) referred to this second attentional function as “selection-for-action”.

The functional coupling of selection-for-perception and selection-for-action has been demonstrated convincingly in several empirical studies on saccadic eye movement preparation (e.g., Hoffman and Subramaniam 1995; Kowler et al. 1995; Deubel and Schneider 1996; Schneider and Deubel 2002). These studies investigated the deployment of visual attention before *single* eye movements to a target position. So, in the study of Kowler et al. (1995), participants were shown displays containing eight pre-masks on a circular array. They were instructed to saccade to the item indicated by a central arrow cue. Simultaneously with the onset of the cue, the pre-masks were replaced by letters, which were

D. Baldauf (✉) · H. Deubel
Department Psychologie,
Ludwig-Maximilians-Universität München,
Leopoldstrasse 13, 80802 Munich, Germany
e-mail: daniel.baldauf@campus.lmu.de
baldauf@psy.uni-muenchen.de

masked again 200 ms later. It was found that the accuracy of letter report was considerably higher for the letters that appeared at the saccade target, than for the letters at movement-irrelevant locations. Similar results were obtained by Deubel and Schneider (1996), Schneider and Deubel (2002). In their studies, participants were first shown string-like arrays of premasks, left and right of fixation. A central colour cue was presented indicating one of the items in the strings as saccade target; the saccade had to be performed when the central cue was removed. Shortly after cue removal, and before saccade onset, a critical discrimination target (digital “E” or “3”) was presented at a certain location in the string among distractors, which was removed after 120 ms. At the end of each trial, participants had to indicate the identity of the discrimination target. The results showed that discrimination accuracy was considerably higher when the discrimination target was presented at the saccade goal than when it was presented at the adjacent positions. This preferential processing of the saccade target was found even when the participants knew in advance the location of the discrimination target, indicating that the coupling of visual attention and saccade target selection is mandatory.

More recently, 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 et al. 1998; Castiello 1996; Schiegg et al. 2003; Deubel and Schneider 2004; Craighero et al. 1998; Bonfiglioli and Castiello 1998; Kritikos et al. 2000).

Movement sequences

The previously mentioned studies all involved experimental situations in which the action had to be directed to a single goal. 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 et al. (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 (Land et al. 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 et al. 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 and Theeuwes 2003) recently investigated the dynamic deployment of attention during the preparation of saccade sequences, however, with basically different results. Gersch et al. (2004) studied attention during inter-saccadic 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 and 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. (2004) 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 and 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 et al. 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 and 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 and 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 et al. 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 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 1a 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 2 asked whether multiple targets are selected before movement onset in even longer eye movement sequences involving three targets. Finally, Experiment 3 used a matching paradigm to study whether multiple movement targets are selected serially or in parallel.

Experiment 1

Method

Participants

Eight students (aged between 24 and 27 years, five females) were paid for their participation in Experiment 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-in. colour monitor with a frame frequency of 100 Hz, at a spatial resolution of $1,024 \times 768$ pixels. The active screen size was 40×30 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 and 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° 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 1a

The sequence of stimuli in a typical trial of Experiment 1a is shown in Fig. 1a. At the beginning of each trial, a display appeared which contained a central fixation cross and a circular arrangement of 12 premask characters (each of which resembled a digital “8”), that were positioned on an imaginary circle with a radius of 5.0° around the central fixation. The horizontal width of the premask characters was 0.6° of visual angle; their height was 0.95° . 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). Simulta-

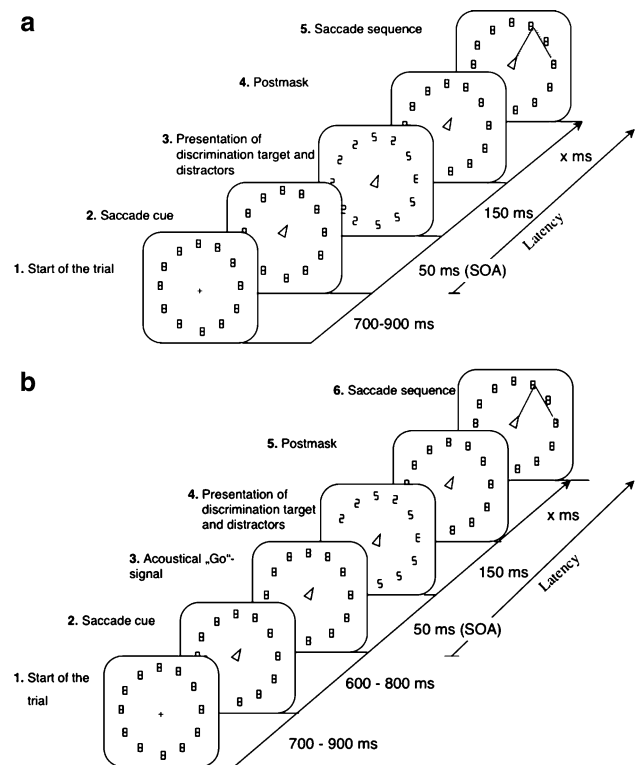


Fig. 1 **a** Stimulus sequence in Experiment 1a. After a random delay the central fixation cross was replaced by a small arrow that indicated the first saccade goal. Upon the onset of this saccade cue, the participants had to perform a double saccade sequences, with the first saccade aimed at the cued target the second saccade directed to the character located two positions further in the clockwise direction. With a SOA of 50 ms the premask characters changed into a critical discrimination target DT (resembling digital “E” or “3”) 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 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

neously 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.

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 “3”. 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 1b

Stimuli and procedure were similar to Experiment 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 600–800 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 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 12 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 "3" was

shown. In total, this led to 84 different conditions (six ST positions \times seven relative DT positions \times two 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° s^{-1} . 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° 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 and Gentleman 1996).

Results

Discarded trials

In Experiment 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 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 shows

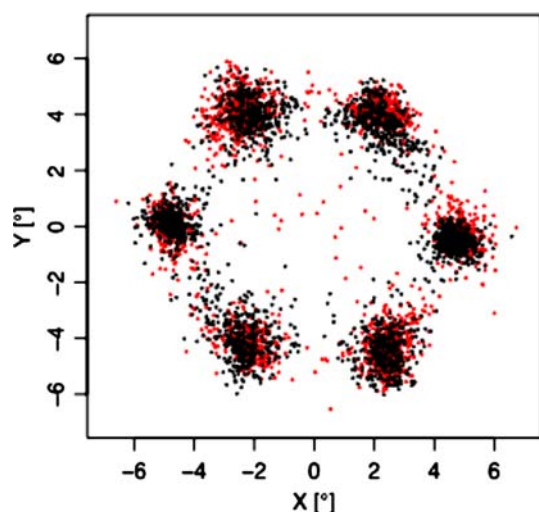


Fig. 2 Final horizontal and vertical eye positions after the first (black) and the second (red) saccade of the double saccade sequences

the endpoints of the first (black) and the second (red) saccades for all eight participants (data from “Experiment 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 0.67° (SE = 0.15°). In Experiment 1b, mean spatial error was 0.69° (SE = 0.19°) and 0.71° (SE = 0.24°).

Mean latency of the initial saccade with respect to cue onset was 281 ms (SE = 25.6 ms) in Experiment 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. ANOVA showed no significant effect of the factor DT position on the latency of the initial saccade of the movement sequence, $F(3, 21) = 1.278$, $P > 0.30$. This is important for the interpretation of the results, since it makes sure that the presentation of the critical discrimination stimulus (“E” vs. “3”) 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 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 Fig. 3 represent discrimination performance as a function of the position of DT relative to the

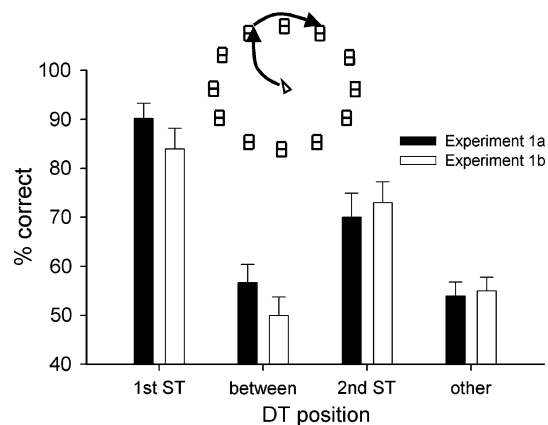


Fig. 3 Discrimination performance in Experiment 1a (filled bars) and Experiment 1b (open bars). The proportion of correct responses in the discrimination task is shown as a function of the location of the discrimination target relative to the saccade goal positions. The bars represent averages across all participants; the error bars show one standard error. Chance level is at 50% correct

saccade target positions in Experiment 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 shows that performance drops to chance at this intermediate location, yielding a discrimination performance of only 56.9% (SE = 2.8%) 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, $t(7) = 6.789$, $P < 0.001$. Also, discrimination performance at the second saccade target position differed significantly from performance at the movement-irrelevant locations $t(7) = 2.916$, $P < 0.001$ and from the performance at the first saccade target, $t(7) = 3.873$, $P < 0.001$. Furthermore, perceptual discrimination at the location *between* both movement targets (condition “between”) differed significantly from both the performance at the first saccade target ($t(7) = 6.248$, $P < 0.001$), and at the second saccade target ($t(7) = 2.375$, $P < 0.049$), but it did not differ from the performance at the movement-irrelevant positions, $t(7) = 0.541$, $P > 0.5$.

The open bars in Fig. 3 represent discrimination performance as a function of the relative DT position, averaged across the nine participants in Experiment 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 1a. A one-way ANOVA was computed for the factor DT position. The analysis yielded a significant main effect of relative DT position, $F(3, 21) = 38.45$, $P < 0.001$. 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, $t(7) = 3.11$, $P > 0.010$. Further, perceptual performance levels at both the first and second movement goal were significantly better than performance at the remaining, movement-irrelevant positions ($t(7) = 6.59$, $P < 0.001$ and $t(7) = 3.48$, $P > 0.01$). The performance at the position between both saccade goals was significantly different from performance at 1st ST, $t(7) = -7.25$, $P < 0.01$, and at 2nd ST, $t(7) = 4.14$, $P < 0.01$, but did not differ from the value at the remaining positions, $t(7) = 0.661$, $P > 0.51$.

Discussion

The results of Experiment 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 and 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 and Yeh 1985). Rather, it is consistent with

the assumption that attentional selection can involve spatially non-contiguous locations.

In Experiment 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 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 of 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 1b, however, shows 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.

Experiment 2

Experiment 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.

Method

The eight participants in this experiment were the same as in Experiment 1. The same stimuli were used. The procedure was also similar to the previous experiment (Experiment 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 Fig. 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, 3, 5, 7, 9 or 11 o’clock). In half of the trials, the discrimination target was the character “E”, in the other half a “3” was shown. In total, this led to 72 different conditions (six cued ST positions \times six relative DT positions \times two 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.

Results

Discarded trials

In this experiment, 9.6% of all trials, had to be discarded because of too short or too long movement latencies.

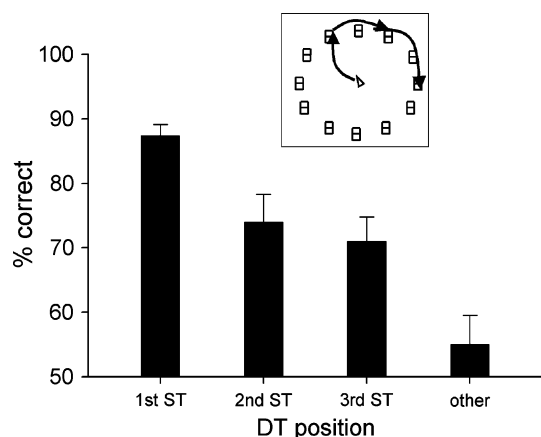


Fig. 4 Experiment 2. Discrimination performance in the discrimination task as a function of the relative location of the discrimination target. The bars represent averages across all participants. The error bars show one standard error

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° ($SE = 0.14^\circ$). 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 ($SE = 24.1$ ms), 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, $F(3, 21) = 1.669$, $P > 0.20$, $F(3, 21) = 2.45$, $P > 0.09$, and $F(3, 21) = 0.07$, $P > 0.97$, 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. “3”) 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 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 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%).

Statistical analysis confirmed a significant effect of the factor DT position on discrimination performance, $F(3, 21) = 22.53$, $P < 0.001$. Pairwise t -tests showed that the difference in performance at the first and the second saccade goal was significant, $t(7) = 2.543$, $P < 0.034$, as well as the difference between the performance values at the first and the third saccade goal, $t(7) = 3.14$, $P < 0.016$. Discrimination performance at the second and the third position did not differ significantly, $t(7) = 0.599$, $P > 0.55$. Importantly, however, discrimination performance at the first, second and third saccade targets each differed significantly from the average performance at the movement-irrelevant locations ($t(7) = 6.02$, $P < 0.001$, $t(7) = 3.478$, $P < 0.002$, and $t(7)$, $P < 0.023$, respectively).

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 indicates that the discrimination performance at the first and the second saccade goals is not markedly deteriorated in comparison to the results of Experiment 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.

Experiment 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 and Theeuwes 2003).

Method

Participants

Seven participants (four females, 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 Fig. 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° 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 (Bouma 1970, 1973; Intriligator and 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. After the presentation of the premask characters for 1,500 ms, 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

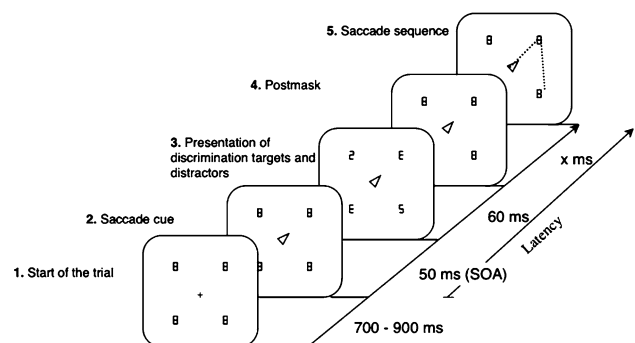


Fig. 5 Stimulus sequence in Experiment 3. The secondary task required a same/different decision on the identity of the two discrimination targets that were presented for 60 ms

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.

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 “3” 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 (four ST positions \times six possible DT arrangements \times two types of DT \times two 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.

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 (50 ms SOA + 60 ms 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° 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° (SE = 0.06°), and the second on average 0.82° (SE = 0.08°) 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, $F(2, 12) = 0.289$, $P > 0.75$, $F(2, 12) = 0.285$, $P > 0.75$, respectively.

Discrimination performance

Figure 6 shows discrimination performance as a function of the positions of the two discrimination targets relative to the saccade goals. 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, $F(2, 12) = 14.8$, $P < 0.001$.

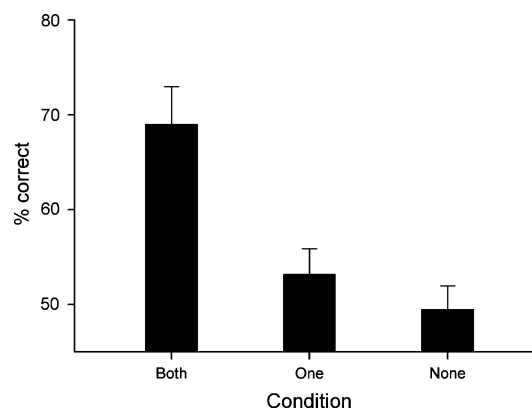


Fig. 6 Performance in the same/different matching task of Experiment 3 as a function of the locations of the two discrimination targets, relative to the saccade goals. Either the locations of both discrimination targets coincided with the saccade goal positions (“Both”), or only one discrimination target 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

Pairwise 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, $t(6) = 3.44$, $P < 0.01$, and $t(6) = 4.47$, $P < 0.01$, respectively.

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 approach, the two discrimination targets were present on the screen for 60 ms only. In line with Kramer and Hahn (1995), Hahn and Kramer (1998) and Godijn and 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 150–200 ms to identify a stimulus that was indicated by a precue and then to reallocate attention covertly to another position (Eriksen and Yeh 1985; Krose and Julesz 1989; Madden 1992). Ward et al. (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 and Nakayama 1993), are limited to peripheral cueing and to specific experimental settings, such as those involving a gap paradigm (see, e.g., Bekkering et al. 1996; Fischer and 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 $P_1 \times P_2 + (1 - P_1) \times (1 - P_2)$. Unfortunately, we did not

determine perceptual performance in a single-target discrimination task for the stimulus arrangement and the presentation times of Experiment 3. However, assuming that perceptual performance at the first and second movement target were similar to those found in Experiment 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 ($= 0.84 \times 0.73 + 0.16 \times 0.27$). This is very close to the value of 0.69 actually found in the matching task of Experiment 3, for the condition where both discrimination targets were presented at the movement-relevant locations.

General discussion

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 and Subramaniam 1995; Deubel and Schneider 1996; Deubel et al. 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 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 extend former evidence reported by Godijn and 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 and 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 important difference between Gersch et al.'s experimental task and the task in our study is that Gersch et al. (2004) 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 and Theeuwes, attention was measured during the interval *before* the onset of the sequence, while Gersch et al. (2004) 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 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.

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 Experiment 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° apart, and appeared at 5.2° 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 and 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 and Hahn (1995). They demonstrated that observers could 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 2, 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).

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 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 and 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.

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 et al. 1997, 2000; Andersen and Buneo 2002; Andersen et al. 1997; Konen et al. 2004; Rizzolatti et al. 1994; Graziano and 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 and Corbetta 2000; Colby 1998; Colby and Goldberg 1999; Rizzolatti et al. 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 et al. 1991). Hahn and Kramer (1998) assumed that LIP may indeed also be crucial for the programming of sequences of saccades (see also, LaBerge and Brown 1989). However, Mazzoni et al. (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 et al. (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 et al. 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 and Fallah 2001, 2004; Cavanaugh and Wurtz 2004; Moore and Armstrong 2003; Wardak et al. 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 et al. (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 et al. 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 and 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 and 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 et al. (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.

Acknowledgments This research was supported by the Deutsche Forschungsgemeinschaft (Graduate Program GRK 1091 to DB and Research Group De 336/2 to HD) and by the Cluster of Excellence “Cognition for Technical Systems”.

References

- Andersen RA, Buneo CA (2002) Intentional maps in posterior parietal cortex. *Ann Rev Neurosci* 25:189–220
- Andersen RA, Snyder LH, Bradley DC, Xing J (1997) Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Ann Rev Neurosci* 20:303–330
- Allport DA (1987) Selection for action: some behavioral and neurophysiological considerations of attention and action. In: Heuer H, Sanders AF (eds) *Perspectives on perception and action*. Lawrence Erlbaum Associates, Hillsdale, pp. 395–419
- Awh E, Armstrong KM, Moore T (2006) Visual and oculomotor selection: links, causes and implications for spatial attention. *Trends Cogn Sci* 10(3):124
- Baldauf D, Wolf M, Deubel H (2006) Deployment of visual attention before sequences of goal-directed hand movements. *Vision Res* 46:4355–4374
- Batista AP, Andersen RA (2001) The parietal reach region codes the next planned movement in a sequential reach task. *J Neurophysiol* 85:539–544
- Bekkering H, Pratt J, Abrams RA (1996) The gap effect for eye and hand movements. *Percept Psychophys* 58:628–635
- Bonfiglioli C, Castiello U (1998) Dissociation of covert and overt spatial attention during prehension movements: selective interference effects. *Percept Psychophys* 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 Res* 13:767–782
- Carrasco M, Penpeci-Talgar C, Eckstein M (2000) Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Res* 40:1203–1215
- Castiello U (1996) Grasping a fruit: selection for action. *J Exp Psychol Hum Percept Perform* 22:582–603
- Cavanaugh J, Wurtz RH (2004) Subcortical modulation of attention counters change blindness. *J Neurosci* 24(50):11236–11243
- Chelazzi L, Corbetta M (2000) Cortical mechanisms of visuospatial attention in the primate brain. In: Gazzaniga MS (ed) *The new cognitive neuroscience*. MIT, Cambridge pp. 667–686
- Colby CL (1998) Action-oriented spatial reference frames in cortex. *Neuron* 20:15–24
- Colby CL, Goldberg ME (1999) Space and attention in parietal cortex. *Ann Rev Neurosci* 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. *J Neurosci* 11:2383–2402
- Craighero L, Fadiga L, Rizzolatti G, Umiltà C (1998) Visuomotor priming. *Vis Cogn* 5:109–125
- Deubel H, Schneider WX (1996) Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res* 36:1827–1837
- Deubel H, Schneider WX (2003) Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. *Ann N Y Acad Sci* 1004:289–296
- Deubel H, Schneider WX (2004) Attentional selection in sequential manual movements, movements around an obstacle and in grasping. In: Humphreys GW, Riddoch MJ (eds) *Attention in action*. Psychology, Hove
- Deubel H, Schneider WX, Paprotta I (1998) Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Vis Cogn* 5:81–107
- Eriksen CW, St. James JD (1986) Visual attention within and around focal attention: a zoom lens model. *Percept Psychophys* 40(4):225–240
- Eriksen CW, Yeh YY (1985) Allocation of attention in the visual field. *J Exp Psychol Hum Percept Perform* 11:583–597
- Fischer B, Weber H (1993) Express saccades and visual attention. *Behav Brain Sci* 16:588–589
- Gersch TM, Kowler E, Doshier B (2004) Dynamic allocation of visual attention during the execution of sequences of saccades. *Vision Res* 44:1469–1483
- Godijn R, Theeuwes J (2003) Parallel allocation of attention prior to the execution of saccade sequences. *J Exp Psychol Hum Percept Perform* 29(5):882–896
- Graziano MSA, Gross CG (1994) Mapping space with neurons. *Curr Dir Psychol Sci* 3:164–167
- Hahn S, Kramer AF (1998) Further evidence for the division of attention among noncontiguous locations. *Vis Cogn* 5:217–256
- Hayhoe M, Land M, Shrivastava A (1999) Coordination of eye and hand movements in a normal environment. *Invest Ophthalmol Vis Sci* 40:S380
- Hoffman JE, Subramaniam B (1995) The role of visual attention in saccadic eye movements. *Percept Psychophys* 57:787–795
- Ihaka R, Gentleman R (1996) R: a language for data analysis and graphics. *J Comput Graph Stat* 5:299–314
- Intriligator J, Cavanagh P (2001) The spatial resolution of visual attention. *Cogn Psychol* 43:171–216
- Kettner RE, Marcario JK, Port NI (1996) Control of remembered reaching sequences in monkey II. Storage and preparation before movement in motor and premotor cortex. *Exp Brain Res* 112:317–358
- Konen CS, Kleiser R, Witsack HJ, Bremmer F, Seitz RJ (2004) The encoding of saccadic eye movements within human posterior parietal cortex. *Neuroimage* 22:304–314
- Kowler E, Anderson E, Doshier B, Blaser E (1995) The role of attention in the programming of saccades. *Vis Res* 35:1897–1916
- Kramer AF, Hahn S (1995) Splitting the beam: distribution of attention over noncontiguous regions of the visual field. *Psychol Sci* 6:381–386
- Kritikos A, Bennett KMB, Dunai J, Castiello U (2000) Interference from distractors in reach-to-grasp movements. *Q J Exp Psychol* 53:131–151
- Krose B, Julesz B (1989) The control and speed of shifts in attention. *Vis Res* 29:1607–1619
- Land MF, 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
- LaBerge D, Brown V (1989) Theory of attentional operation in shape identification. *Psychol Rev* 96:101–124
- Logan GD (2005) The time it takes to switch attention. *Psychon Bull Rev* 12(4):647–653
- Mackeben M, Nakayama K (1993) Express attentional shifts. *Vis Res* 33(1):85–90

- Madden D (1992) Selective attention and visual search: revision of an allocation model and application to age differences. *J Exp Psychol Hum Percept Psychophys* 18:821–836
- Mazzoni P, Bracewell RM, Barash S, Andersen RA (1996) Motor intention activity in the macaque's lateral intraparietal area. I. Dissociation of motor plan from sensory memory. *J Neurophysiol* 76(3):1439–1456
- Medendorp WP, Goltz HC, Vilis T (2006) Directional selectivity of BOLD activity in human posterior parietal cortex for memory-guided double-step saccades. *J Neurophysiol* 95:1645–1655
- Moore T, Armstrong KM (2003) Selective gating of visual signals by microstimulation of frontal cortex. *Nature* 421:370
- Moore T, Fallah M (2004) Microstimulation of the frontal eye field and its effects on covert spatial attention. *J Neurophysiol* 91:152–162
- Moore T, Fallah M (2001) Control of eye movements and spatial attention. *Proc Nat Acad Sci* 98(3):1273–1276
- 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
- Neumann O (1987) Beyond capacity: a functional view of attention. In: Heuer H, Sanders AF (eds) *Perspectives on perception and action*. Lawrence Erlbaum, Hillsdale, pp. 361–394
- Posner MI (1980) Orienting of attention. *Q J Exp Psychol* 32:3–25
- Rizzolatti G, Riggio L, Sheliga BM (1994) Space and selective attention. In: Umiltà C, Moscovitch M (eds) *Attention and performance XV. Conscious and nonconscious information processing*. MIT, Cambridge, pp. 231–265
- Schiegg A, Deubel H, Schneider WX (2003) Attentional selection during preparation of prehension movements. *Vis Cogn* 10(4):409
- Schneider WX (1995) VAM: a neuro-cognitive model for attention control of segmentation, object recognition and space-based motor action. *Vis Cogn* 2:331–374
- Schneider WX, Deubel H (2002) Selection-for-perception and selection-for-spatial motor-action are coupled by visual attention: a review of recent findings and new evidence from stimulus-driven saccade control. In: Prinz W, Hommel B (eds) *Attention and performance XIX: common mechanisms in perception and action*. Oxford University Press, Oxford, 609–627
- Snyder LH, Batista AP, Andersen RA (1997) Coding of intention on the posterior parietal cortex. *Nature* 386:167–170
- Snyder LH, Batista AP, Andersen RA (2000) Intention-related activity in the posterior parietal cortex. *Vision Res* 40:1433–1441
- Treisman A, Gelade G (1980) A feature-integration theory of attention. *Cogn Psychol* 12(1):97–136
- Wardak C, Ibos G, Duhamel J, Olivier E (2006) Contribution of the monkey frontal eye field to covert visual attention. *J Neurosci* 26(16):4228–4235
- Ward R, Duncan J, Shapiro K (1996) The slow time course of visual attention. *Cogn Psychol* 30:79–109
- Wolf W, Deubel H (1997) P31 phosphor persistence at photopic luminance level. *Spat Vis* 4:323–333