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Abstract:

This deliverable reports data on the effect of modified motor parameters on visual localization of fragments. In two studies we modifed saccade amplitude by saccadic adaption and measured the influence on the localization of visual targets. In the first study, different types of saccades (reflexive vs. scanning) are shown to differently affect visual localization. The amount of effect depends on the temporal properties of the fragments that have to be localized (stationary vs. flashed). In the second study, adapation of saccade motor parameters is shown to influence visual localization even when subjects remain in fixation, demonstrating the generalization of the sensorimotor space coding. These results provide a knowledge base for the implementation of sensorimotor laws in an action-minded spatial representation.

Contents

1 Introduction

1.1 The Visual System

The visual system is regarded as the dominant sensory system in humans. It provides in an outstanding manner 3D data of the environment. Whereas taste and touch provide local information only, the visual information is far reaching, in contrast to the auditory system highly topographically ordered and of outstanding resolution. A huge amount of visual data would have to be processed and stored in very short time if the whole scene would be detected at once. Therefore, a concept of selected processing becomes attractive. For this, a motor system is needed, whose duty it is to target the center of the receptor at the fragment of interest. This strategy constitutes new requirements to the binding of fragments. A huge amount of patches of visual data is received. The only information available to bind between these fragments are the motor parameters. Thus, a strong interaction between visual and motor parameters is essential for the processing of visual information to develop a robotic system for interactive vision (Objective I) and a model of a multisensory representation of the 3D space (Objective II).

1.2 Saccades & Saccadic Adaptation

To make an effective system interconnecting patches of information, different requirements have to be fulfilled by the connecting motor system. On the one hand, the time between two measurements is to be reduced. This means that the motor system has to be able to conduct fast movements. On the other hand, high accuracy is needed to bind the different fragments in a sufficient way.

These fast eye movements are called saccades. They occur about every 300 msec, reach speeds up to about 500 deg per second and are of outstanding accuracy. They bring a certain fragment containing an object or piece of interest, in the fovea. Since because of the speed of the saccade no visual feedback is available during the movement, the system is relying on internal estimations. It was found that the reliability of the saccadic system is due to at least one control mechanism, which monitors the accuracy of the saccadic system by correcting for errors in landing position of the eye by changing motor parameters, which influence all following saccades. By this constantly awake controlling system the effectivenes and feasiblity are guaranteed.

Saccades and their motor parameters therefore bind fragments and provide the essential link between visual fragments. In its role connecting motor and sensory systems in a unique way, the saccadic system is object of different studies.

One of the methods of choice to activate these control mechanisms of the saccadic system is the McLaughlin adaptation paradigm. Saccadic adaptation occurs when the saccade target is systematically displaced during execution of the saccade (McLaughlin, 1967). This displacement induces a visual error after the saccade which is corrected by a short subsequent saccade. Over the course of successive trials the amplitude of the primary saccade is gradually changed to immediately reach the displaced target location.

1.3 Interdependence of sensory and motor parameters and their role in EYESHOTS

The interplay between vision and saccades is a prime example of an action-perception coupling: saccades are made to acquire new visual information, and vision, in return, is used to localize the next saccade target. Therefore, an interaction of motor and visual parameters on fragment location is essential for the processing of visual information and for the construction and design of the bio-inspired robotic system. Thus, 3D vision via interactive stereopsis is based on eye movements and the existence of visuomotor representations (Objective I). Updating of internal representations of spatial relations requires binding processes across visual fragments. Therefore, experimental determination of sensorimotor interdependencies can be considered as a basis for a model of a multisensory egocentric representation of 3D space (Objective II). As described in the Annex I, motor commands of the oculomotor system will be used in the model to update egocentric relationships and object-to-object relationships. Furthermore, the connections between sensory and oculomotor parameters will be needed for the fusion of arm and eye movements. This is an important contribution to the knowledge of sensorimotor laws which are to be included in the model. In the end, the binding of fragments achieved by sensorimotor relations is the basis for binding objects.

1.4 Transfer of motor adaptation to visual localization of fragments

As described in Task 5.3 the role of the interdependence of visual and motor parameters can be measured in psychophysical experiments, in which saccadic eye movements and visual localization of fragments are combined. The following two studies examine the aspect of binding fragments by considering, first, the transfer of fragment location information over a saccade in an adapted situation, and, second, the effects of motor adaptation on localization of visual stimuli independent of a saccade. In the second study direct influences of motor parameter adaptation on visual parameters can be examined. The results of the two studies can be considered as a basis for the adaptation experiments in monkeys at UNIBO. Furthermore, the results can be used in WP4 for merging perception-related and action-related visual information, generating visuo-motor descriptors of reachable objects and finally constructing a global awareness.

2 Study I: Localization of fragments after a saccade

2.1 Introduction

Saccadic adaptation influences the localization of visual stimuli. Awater et al. (2005) asked subjects to report the location of a peri-saccadic flash after execution of an adapted saccade. Flashes that occurred before the saccade were systematically shifted in the direction of adaptation. This mislocalization can be observed several hundred milliseconds before the saccade and is distinct from other peri-saccadic mislocalizations such as peri-saccadic compression (Georg and Lappe, 2009). It occurs for verbal as well as for pointing responses (Bruno and Morrone, 2007). The mislocalization is confined to the area near the saccade target (Awater et al., 2005) and matches the spread of adaptation around the saccade target, the so-called saccade adaptation field (Collins et al., 2007). Investigations of the spatial (Collins et al., 2007) and temporal (Georg and Lappe, 2009) properties of the mislocalization have shown that both, visual reference information from the post-saccadic target image and control parameters of the saccade contribute to the magnitude and direction of the mislocalization. Furthermore, a mismatch between the efference copy signal and the adapted saccade (Bahcall and Kowler, 1999) or an adaptation of eye position signals (Hernandez et al., 2008) may be involved.

While saccadic adaptation is known to rely strongly on cerebellar and other subcortical structures (Desmurget et al., 1998; Robinson and Fuchs, 2001; Catz et al., 2008; Golla et al., 2008), the adaptation-induced mislocalization suggests effects of adaptation on the cortical level, or at least feedback from cerebellar or subcortical structures onto cortical localization mechanisms (Awater et al., 2005; Gaymard et al., 2001). Involvement of different cortical pathways in saccadic adaptation has been proposed to account for the specificity of adaptation to different saccade types in humans (Erkelens and Hulleman, 1993; Deubel, 1995; Hopp and Fuchs, 2004; Alahyane et al., 2007).

One particular distinction occurs between reactive and scanning saccades. Reactive saccades are visually triggered by a suddenly appearing target, and are believed to receive target localization signals from parietal pathways to the SC and the brainstem saccade generator (Pierrot-Deseilligny et al., 1991; Gaymard et al., 2003; Müri and Nyffeler, 2008; Schraa-Tam et al., 2009; Mort et al., 2003). The term scanning saccades (Deubel, 1995; Cotti et al., 2007) describes saccades that are performed in the voluntary scanning of a stationary visual scene, in which target selection is not driven by the salient onset of a stimulus but rather by task demands and voluntary selection between multiple targets. Such saccades have also been called internally triggered (Erkelens and Hulleman, 1993; Fujita et al., 2002) or voluntary (Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Walker and McSorley, 2006) saccades. Targeting of these saccades is believed to involve pathways from frontal cortex to SC and brainstem (Rivaud et al., 1994; Heide and Kömpf, 1998; Müri and Nyffeler, 2008; Schraa-Tam et al., 2009).

Evidence for a separation between the pathways for reactive and scanning saccades is seen in transfer tests of adaptation (Erkelens and Hulleman, 1993; Deubel, 1995; Fujita et al., 2002; Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2007). Adaptation of reactive saccades induces little adaptation of voluntary saccades. Transfer rates are between 6 and 56 %. Therefore, the adaptation must occur mostly in the reactive pathway. Adaptation of scanning saccades, on the other hand, induces some adaptation also of reactive saccades. Transfer rates are between 24 and 74 %. Thus, adaptation occurs in both the scanning and the reactive pathways, but to different degrees.

We used the differences between reactive and scanning saccades to investigate the interplay between visual localization and saccade targeting. First, we wanted to know whether the adaptation-induced shift occurs similarly for both saccade types, or whether it is specific to a particular saccade type. This would inform us about the pathways which are involved in the adaptation-induced mislocalization. Second, we wanted to know whether the mislocalization induced in a particular saccade paradigm is specific to the visual target properties of the associated pathway, i.e. flashed stimuli for reactive saccades and stationary stimuli for scanning saccades. This would mean that adaptation and mislocalization share pathways that process particular target signals.

To answer these questions we conducted adaptation experiments separately with reactive and voluntary saccades, and tested, in each case, mislocalization of flashed targets and of targets that were continuously visible from the onset of a trial until the subject started the saccade.

2.2 Methods

2.2.1 Adaptation of reactive saccades

The subject was seated 57 cm in front of a 22” computer monitor (Eizo FlexScan F930) with the head stabilized by a chin rest. The visible screen diagonal was 20”, resulting in a visual field of 40 deg x 30 deg. Stimuli were presented on the monitor with a vertical frequency of 120 Hz at a resolution of 800 x 600 pixels. The room was completely dark. To avoid visibility of the screen borders the display monitor was covered with a transparent foil that reduced the luminance by about 2 log units. Eye movements were monitored by the Eyelink 1000 system (SR Research, Ltd., Canada), which samples gaze positions with a frequency of 1000 Hz. Viewing was binocular but only the dominant eye was recorded. The system detected start and end of a saccade when eye velocity exceeded or fell below 22 deg/s and acceleration was above or below 4000 deg/sec^2.

Figure 1A and B depict the procedure for adaptation of reactive saccades. A fixation point (1 deg x 1 deg, luminance 0.06 cd/m^2, red color), illustrated by the square in Figure 1A, was first placed 5 deg to the right of the left screen border. The subject had to establish and maintain fixation at this point. The circle in Figure 1A indicates the gaze of the subject. After 1 s the fixation point was extinguished and a saccade target (red, 1 deg x 1 deg, luminance 0.06 cd/m^2) suddenly appeared 30 deg to the right of the fixation point. The subject was instructed to make a saccade to the target as quickly as possible. Eye position was monitored online. As soon as the eye crossed an invisible border at 2.5 deg to the right of the fixation point the saccade target was stepped back by 6 deg. In the initial trials this back step caused a visual error at the end of the saccade. With increased number of trials this error is reduced such that the eye lands closer to the back-stepped target location (Figure 1B). After 80 adaptation trials, when the subject already had begun to adapt, the back-step was increased to 9 deg to increase the final amount of adaptation.

In order to ensure that the subject really reacted to the sudden appearance of the target, and did not pre-plan the saccade, some trials were randomly interspersed (probability 0.33) in which the saccade target appeared 20 deg above or below the fixation point. These trials were checked for compliance with the instruction, but were not used for adaptation, and did not enter into the data analysis. They did not interfere with adaptation because adaptation is direction specific (Frens and Van Opstal, 1994; Albano, 1996). Moreover, in order to counteract dark-adaptation of the subject these trials were followed by a 1 s period in which the screen turned white (luminance 0.6 cd/m^2) while the subjects had to maintain fixation at the target location.

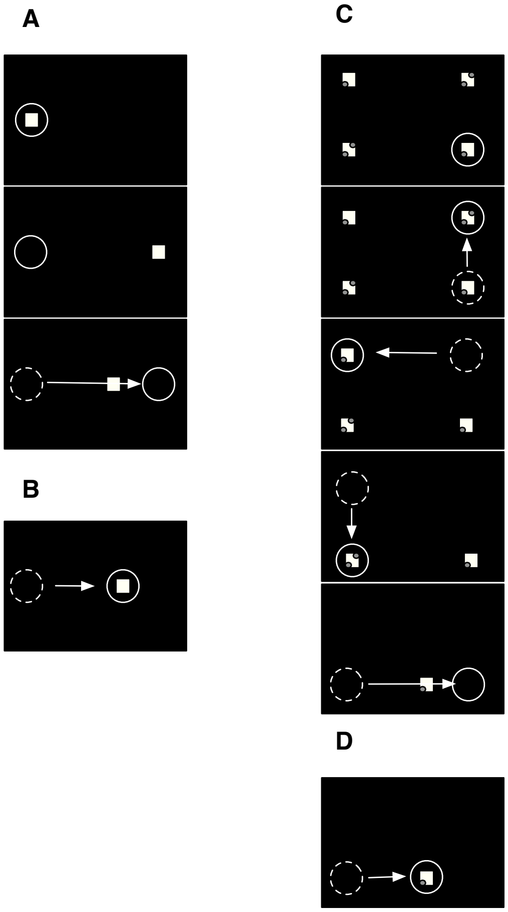

Figure 1: A: experimental procedure for reactive saccade adaptation. At the beginning of the trial (top panel) a fixation point (square) is presented near the left screen border. The subjects gaze (circle) is directed to the fixation point. After 1000 ms (middle panel) the fixation point disappears and a saccade target appears 30 deg to the right of the fixation point. The subject initiates the saccade to the target. When the saccade onset is detected (bottom panel), the saccade target is displaced, inducing a visual error after the saccade. B: after several adaptation trials the saccade amplitude becomes shorter. The saccade ends on the displaced target and the visual error after the saccade is reduced. C: experimental procedure for scanning saccade adaptation. At trial onset (top panel) four saccade targets (squares) are presented. The subject fixates the bottom right target (circle). At a voluntary pace, the subject scans the targets in a counterclockwise manner. As the subject executes each saccade the previously inspected target is extinguished. Adaptation takes place during the saccade from the bottom left to the bottom right target (bottom panel). When the onset of the saccade is detected the bottom right target is displaced to the left, inducing a visual error after the saccade. D: after several adaptation trials the saccade amplitude is adapted to the displaced target location.

2.2.2 Adaptation of scanning saccades

The procedure for scanning saccades followed the paradigm introduced by Deubel (1995). Four saccade targets (1 deg x 1 deg, luminance 0.06 cd/m^2, red color) were presented at trial onset (Figure 1). The saccade targets were arranged in a rectangle with a horizontal distance of 30 deg and a vertical distance of 20 deg. The left edge of the rectangle was 5 deg to the right of the left screen border. Subjects began by fixating their gaze (circle) at the bottom right target. They then had to scan the other saccade targets in a counterclockwise manner at a voluntary pace. In order to ensure that subjects truly scrutinized each target, the saccade targets contained small discrimination dots, either one or two, that could be seen only by foveal inspection of the target. The subject had to count how often a pair of two discrimination dots was present in a trial.

While the subject made saccades from one target to the next the previously inspected targets were extinguished. The top right target was turned off during the saccade from the top right target to the top left target. The top left target was turned off during the saccade to the bottom left target. The bottom left target was turned off during the final saccade from the bottom left to the bottom right target. Each target was extinguished when the eye had travelled a distance of 2.5 deg along the path of the respective saccade. When the subject performed the final saccade, i.e. the 30 deg rightward saccade from the bottom left target to the bottom right target, only the final target (bottom right) remained on the screen. This saccade was adapted. The bottom right target was shifted 6 deg to the left as soon as the eye crossed the invisible border at 2.5 deg to the right of the bottom left target. After 80 consecutive adaptation trials the displacement was increased to 9 deg. The scanning adaptation procedure therefore differed from the reactive adaptation procedure in the way in which the saccades were initiated, but it was similar in terms of the metric of the adapted saccade, the stimuli visible at the time of adaptation, and the timing and size of the target backstep.

Reactive and scanning saccades are known to differ strongly in latency (Deubel, 1995; Cotti et al., 2007). We therefore used latency differences in the two conditions as a first test of whether we were successful in eliciting different saccade types. Latency in the reactive case was measured from the onset of the target. Since for scanning saccades there is no target onset, latency for scanning saccades was calculated from the onset of the preceding fixation. This measure includes the fixation duration during which the data for the discrimination task must be gathered. It is thus not directly equivalent to the latency in the reactive case, but it is commonly used as a check for differences between saccade types (Deubel, 1995; Cotti et al., 2007), and will serve for this purpose here as well. Saccade latencies differed between the reactive and the voluntary saccade trials as expected. The mean reactive saccade latency over the reactive saccade adaptation sessions was 210 ± 56 ms. The mean scanning saccade latency over the scanning saccade adaptation sessions was 515 ± 113. We also checked latencies in transfer trials (described later in detail) in which reactive saccades were performed after scanning saccade adaptation, and vice versa. The mean latency of reactive saccades performed in these transfer trials was 224 ± 44. The mean latency of scanning saccades performed in the transfer trials was 484 ± 123 ms. A two-way repeated measures ANOVA revealed a significant difference between saccades types in both regular and transfer trials ($F = 75.41$, $p < 0.01$). The different latency suggests that we were successful in eliciting different saccades types in the different conditions.

2.2.3 Localization

Localization was tested before and after adaptation, while subjects performed normal and adapted saccades, respectively. Two types of localization trials were run. One used a flashed localization probe, like the targets used for reactive saccades. The other used a stationary localization probe like the targets used for scanning saccades. These stimuli were designed to imitate the temporal properties of the saccade targets that trigger reactive and scanning saccades.

In other respects the probe stimuli were visibly distinct from the saccade target to avoid confusion in the localization task. The flashed localization probe was a small bar (0.3 deg x 4 deg, luminance 0.2 cd/m^2). The probe was presented for 20 ms at a randomly chosen horizontal position in a range of 2 deg around the saccade target (i.e., between 28 and 32 deg).

The vertical position of the bar was the same as that of the saccade target. In reactive saccade trials, the bar was flashed 50 ms after the appearance of the saccade target, i.e. about 150 ms (depending on saccade latency) before the reactive saccade. In scanning saccade trials the bar was flashed when the eye tracker detected that the eye position was on the bottom left saccade target, i.e., before the saccade that was adapted. In both cases, trials in which the bar was flashed less than 100 ms before saccade onset were omitted from analysis because we did not want any interference from peri-saccadic mislocalizations (Georg and Lappe, 2009). Furthermore, occasional trials in which subjects failed to notice the bar were also omitted from analysis. Subjects indicated when they did not see the bar by clicking with the mouse pointer in the lower right corner of the screen. Based on these two criteria, 6% of the data had to be omitted from analysis. If for any subject this resulted in less than ten trials in either the target–off, the target–on, or the transfer trials that subject repeated the recording session and we collapsed the data from both sessions.

The stationary localization probe was identical to the flashed probe but was presented from trial start until the occurrence of the saccade, i.e. when the eye tracker detected that the eye had travelled 2.5 deg along the path of the saccade. Thus, in the reactive saccade trials the bar was continuously visible throughout the 1 s fixation period and during the latency of the saccade. In the scanning saccade trials, the bar was continuously visible throughout the time that the subject took to look at all but the final target.

The task of the subject in the localization trials was to indicate the location of the bar with a mouse pointer. The pointer appeared 1000 ms after the saccade near the bottom of the screen at a randomly assigned horizontal position between 35 deg and 40 deg. The localization error was calculated as the deviation of the mouse click position from the position where the bar was presented.

Normally, because the localization was performed in conjunction with the execution of normal or adapted saccades, the saccade target either remained stationary or jumped back in the respective cases. Thus, it was visible after the saccade and during the reporting with the mouse. Therefore, the saccade target might serve as a visual reference for the localization task. To test for the influence of the post-saccadic target reference we included also trials in which the target was turned off during the saccade. In these target-off trials no visual references were available after the eye landed.

2.2.4 Sequence of events during a single adaptation and localization session

A single session consisted of one type of saccade adaptation (reactive or scanning) with one type of localization task (flashed or stationary). Therefore, each subject had to complete four sessions: reactive saccade adaptation with flashed localization probes, reactive saccade adaptation with stationary localization probes, scanning saccade adaptation with flashed localization probes, and scanning saccade adaptation with stationary localization probes. These four sessions were run on different days and in counterbalanced order across subjects.

The basic structure of trial blocks was the same for each session (Figure 2). The session started with a block of 40 pre-adaptation trials of the respective saccade type. These trials allowed to calculate saccade amplitudes as a baseline before adaptation. Moreover, all pre-adaptation trials included the localization task to record a baseline for localization error. Trials in which the saccade target was turned off during execution of the saccade (target-off trials) were randomly interspersed (probabilty 0.33)

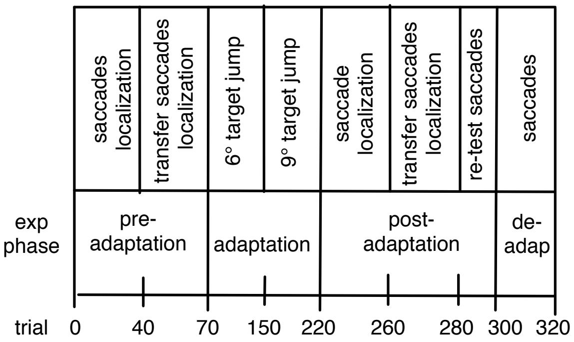

Figure 2: Trial structure for a single saccade adaptation session. In the pre-adaptation phase saccades of the to-be-adapated type and of the transfer type are performed, together with the localization task. In the adaptation phase, only adaptation saccades are performed without localization. About halfway during the adaptation phase the target backstep is increased from 6 deg to 9 deg to increase the final amount of adaptation. In the post adaptation phase adapted saccades and transfer saccades are performed together with the localization task. A small number of deadaptation saccades end the session.

with trials in which the saccade target remained illuminated (target-on trials).

Next came a block of 30 pre-adaptation trials of the opposite saccade type (i.e. scanning saccades for reactive saccade adaptation sessions, and reactive saccades for scanning saccade adaptation sessions). These trials served as a baseline for the transfer test between saccade types. The localization task was included in all of these trials. Target-off trials in which the saccade target was turned off during execution of the saccade were randomly interspersed (probabilty 0.33) with target-on trials in which the saccade target remained illuminated.

The third block consisted of 150 adaptation trials. Saccade adaptation was induced stepwise in order to avoid that subjects notice the saccade target backstep. In the first 80 of the adaptation trials the target stepped back 6 deg to the left of the initial saccade target position. In the remaining 70 trials the back step was increased to 9 deg. These trials did not contain a localization task. They only served to establish adaptation.

The fourth block (post-adapatation, 40 trials) continued with further adaptation trials but also included the localization task. Target-on and target-off conditions were randomly intermixed. The saccade amplitude data from the target-off trials was used to measure the amount of adaptation.

Then, a block of 20 transfer-test trials was performed, in which saccades of the opposite type had to be performed, i.e. scanning saccades after reactive saccade adaptation and reactive saccades after scanning saccade adaptation. These trials served to measure the amount of adaptation transfer from the adapted saccade type to the other saccade type. The localization task was also included to measure the amount of mislocalization transfer. In all trials, the saccade target was turned off during execution of the saccade to avoid deadaptation.

Thereafter, the opposite saccade type was tested again in 20 retest trials. The aim of the retest trials was to check for any deadaptation of saccade amplitude size after the transfer-test trials. Again, to prevent deadaptation the saccade target was turned off during execution of the saccade.

Finally, in 20 deadaptation trials the saccade target remained in its initial position in order to help the subject to deadapt before leaving the experiment.

2.2.5 Participants

Nine subjects, 5 male, 4 female (1 author, 8 naive subjects, mean age = 23 years) participated in all of the experiments. All subjects were students from the Psychology Departement and had normal or corrected-to-normal vision. Subjects gave informed consent. All subjects underwent all experimental conditions. The experiments were carried out along the principles laid down in the declaration of Helsinki.

2.3 Results

We performed adaptation experiments with reactive and voluntary saccades. After adaptation we measured the adaptation-induced mislocalization of probe stimuli. We used two different sets of probes, one flashed and one stationary, to study whether the mislocalization is specific to the visual properties of the associated saccade targeting pathway. We will first report measurements of the saccade amplitude adaptation and thereafter the results of the localization task.

2.3.1 Saccadic adaptation and transfer

Figure 3A shows saccade amplitudes over a single session of reactive saccade adaptation. Trials in which reactive saccades were performed are shown in red. Pretest and transfer-test trials in which scanning saccades were performed are shown in blue. The first 40 trials were pre-adapation reactive saccade trials in which the subject performed normal reactive saccades to a suddenly appearing target at 30 deg. The

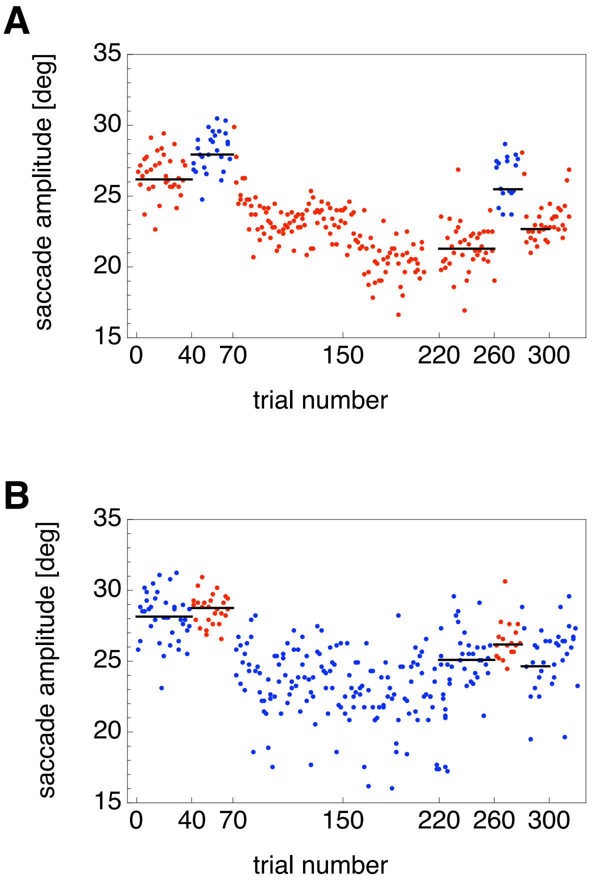

Figure 3: A: example adaptation curve for reactive saccades. Reactive saccades are plotted in red, intermixed scanning saccades in blue. B: example adaptation curve for scanning saccades. Scanning saccades are plotted in blue, intermixed reactive saccades in red. The example for reactive adaptation contained flashed localization trials. The example for scanning adaptation contained stationary localization trials.

target remained at its position and did not jump during the saccade. These saccades were hypometric with a median at 26.43 deg(black horizontal line), which is normal for saccades of this size.

The next 30 saccades (from trial 41 to trial 70) were pre-adapation scanning saccades, which were performed as part of a scanning sequence across four targets as described in Methods. The saccade shown is the last of those four saccades. It is directed from a target on the left to a stationary target 30 deg to the right, and matches the reactive saccade in terms of target direction and amplitude. The only difference to the reactive saccade is that this saccade is conducted to a target that was present on the screen during the entire scanning series whereas the reactive target suddenly appeared and triggered saccade execution. Like the reactive pre-adaptation saccades (first 40 trials) the scanning pre-adaptation saccades (trials 41 to 70) were somewhat hypometric in this subject. The median (black line) was 28.25 deg.

Trials 71 to 220 were reactive saccade adaptation trials in which the target was displaced to the left during the saccade. The displacement was initially 6 deg and was increased to 9 deg from trial 150 onward. The saccade amplitude decreases gradually over the adaptation period towards a value close to the displaced target location at 21 deg.

The amount of adaptation was measured in the post-adaptation trials (221 to 260). The median saccade amplitude in the post-adaptation trials in this session was 21.39 deg (black line in trials 221 to 260 in 3A).

The post-adaptation trials were followed by transfer-test trials (trials 261 to 280). In these trials, scanning saccades were performed in the identical procedure to that in the pre-adaptation scanning trials (41 to 70). The amplitude of these scanning saccades showed little indication of adaptation. The median (black line) was 26.31 deg.

After the transfer-test trials, which often showed less adaptation for the scanning than for the reactive saccades, we checked that reactive saccades were still adapted. This was done in retest trials (numbers 281 to 300) that were identical to the target-off trials of the post-adaptation reactive block (trials 261 to 280). The median amplitude in these retest trials was 22.61 deg. Thus, a large amount of adaptation for reactive saccades was retained across the block of scanning saccades that had shown little adaptation. Lastly, a few deadapation saccades (301 to 320) were performed to start extinguishing the adaptation. In these trials, the target did not jump during the saccade but stayed at the initial position. These trials were not used for data analysis.

Comparison of the saccade amplitude data from the different phases of the session clearly shows that adaptation occurs during the reactive adaptation trials and is retained through the post- and retest phases, while scanning saccades in the transfer trials showed little modification of saccade amplitude. To quantify the amount of adaptation of the reactive saccades we subtracted the average of the median saccadic amplitudes in the the post-adaptation (21.39 deg) and the retest (22.61 deg) trials from the median saccadic amplitude in the reactive pre-adaptation trials (26.43 deg). For the data of Figure 3A this gave an adaptation of 4.4 deg. The amount of adaptation to scanning saccades in the transfer condition was calculated from the difference between the median saccadic amplitudes in the scanning pre-adaptation trials (28.25 deg) and the transfer-test trials (26.31 deg). This gave a transfer adaptation of 2 deg.

Saccade amplitudes over a single session of scanning saccade adaptation are shown in Figure 3B. Scanning saccade trials are shown in blue. Pretest and transfer-test trials, in which reactive saccades were performed, are shown in red. The first 40 trials were pre-adaptation scanning saccade trials. As in the scanning pre-adaptation trials of the reactive saccade adaptation session (blue dots in Figure 3A) the saccades prior to adaptation are slightly hypometric with a median amplitude of 28.51 deg. The following 30 trials (41 to 70) were pre-adaptation reactive saccades. They were elicited in the same way as in the reactive saccade adaptation sessions and differed from the scanning saccade trials only in that the saccade target was suddenly appearing. Median saccade amplitude was 28.7.

Adaptation of scanning saccades began with trial 71. An initial 6 deg jump displaced the saccade target from 30 deg to 24 deg for the next 80 trials (71 to 150). From trial 151 to 220, the size of the saccade target jump was increased to 9 deg displacing the target to 21 deg. After adaptation median scanning saccade amplitude in the post-adaptation trials (trials 221 to 260) was 24.91 deg, indicating an adaptation of 3.6 deg.

Reactive saccade amplitudes in the transfer-test trials (red dots, trials 261 to 280) were partially affected by the adaptation of scanning saccades. The median amplitude size in the transfer-test trials was 26.21 deg, indicating an adaptation of 2.49 deg. Scanning saccades performed afterwards in the retest trials (trials 281 to 300) remained largely adapted. The median amplitudes was 24.48 deg, close to the median of the post-test trials (24.91 deg). Finally, trials 301 to 320 were deadaptation trials in which the saccade target remained in its initial position at 30 deg.

The median saccade amplitudes in the reactive and the voluntary pre-adaptation trials in this subject differed slightly across sessions. In Figure 3A reactive saccades are more hypometric than scanning saccades, whereas this is not the case in Figure 3B. Such differences occurred in some subjects but were not consistent. We calculated the median of the reactive and voluntary saccade amplitudes from all pre-adaptation trials for each subject. An one way paired t-test revealed no significant difference between the reactive and the voluntary saccade pre-adaptation amplitudes.

The example results from Figure 3 show that adaptation occurred for both saccade types, and that transfer between the saccade types was limited. Figure 4 shows adaptation and transfer amounts for reactive and scanning sessions averaged across all subjects. After reactive saccade adaptation (Figure 4A), saccadic amplitudes to reactive targets were decreased on average by 4.9 deg. Amplitudes of scanning saccades in that situation (transfer-test) were decreased by only 1.6 deg. After scanning saccade adaptation (Figure 4B), saccadic amplitudes to scanning targets were decreased by 4.4 deg, and transfer saccades to reactive targets were decreased by 1.6 deg. A two-way repeated measures ANOVA confirmed a significant reduction in the transfer condition but no difference between saccade types ($F = 100.12$,$p < 0.01$).

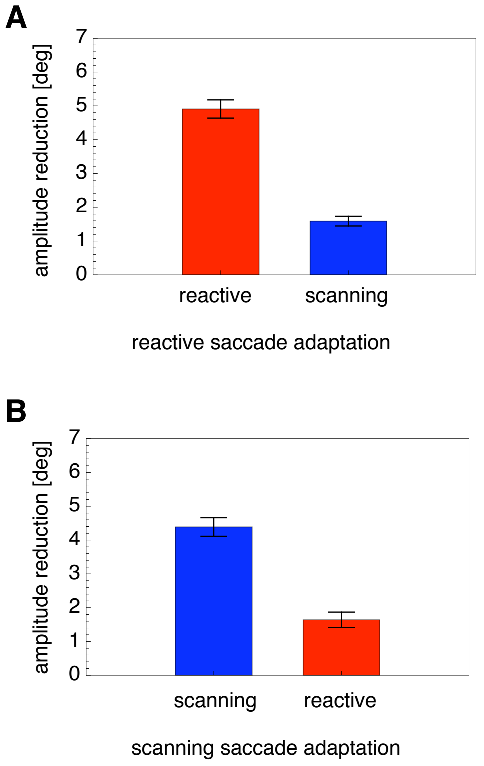

Figure 4: A: average amplitude reduction after reactive saccade adaptation for reactive saccades (red) and for scanning saccades (blue). B: average amplitude reduction after scanning saccade adaptation for reactive saccades (red) and for scanning saccades. In both cases there is strong adaptation and small transfer to the other saccade type. Error bars are standard errors.

We also tested whether the amount of transfer of adaptation from one saccade type to the other was different between reactive and scanning saccade adaptation sessions. We therefore calculated the percentage of transfer for each subject (amplitude decrease in transfer trials / amplitude decrease in adaptation trials *100). Average transfer across all subjects was 36% from the adaptation of reactive saccades to the amplitude of scanning saccades and 43% from the adaptation of scanning saccades to the amplitude of reactive saccades. The transfer from scanning to reactive was, therefore, somewhat higher then from reactive to scanning, but the difference failed to reach significance, ($p = 0.06$, one-sided paired t-test).

The above analysis of saccade amplitude reduction shows that we adapted reactive and scanning saccades individually, and that adaptation of one saccade type led to only partial adaptation of the other. This is consistent with earlier reports of limited transfer between reactive and voluntary saccades. Reactive saccade adaptation has been found to transfer little (between 6 % and 56 %) to scanning (Deubel, 1995; Alahyane et al., 2007; Cotti et al., 2007) and other types of voluntary saccades

(Erkelens and Hulleman, 1993; Deubel, 1995; Fujita et al., 2002; Collins and Dore-Mazars, 2006). Our findings are fully consistent with this. Adaptation of scanning saccades, on the other hand, also transfers only partially to reactive saccades, but the reported transfer rates are usually higher (between 24 % and 74 %) (Deubel, 1995; Alahyane et al., 2007; Cotti et al., 2007). Therefore, the transfer between reactive and scanning saccades has been called asymmetric: small from reactive to scanning and larger from scanning to reactive. The transfer from scanning to reactive saccades in our data is near the lower end of the range reported in the literature. However, it is still larger than the transfer from reactive to scanning saccades, and, thus, consistent with an asymmetric transfer. Most important is, however, that the limited transfer in either direction is indicative of adaption of different saccade targeting pathways, which is a prerequisite for the study of differences in mislocalization that we report next.

2.3.2 Localization results

In order to test influences of saccade adaptation on visual localization, a localization task was included in the trials before and after adaptation of each saccade type. In every adaptation session, localization was tested both in trials in which the adapted saccade type was performed, and in trials in which the opposite saccade type was performed. The subject had to indicate the perceived bar position with the mouse pointer after execution of the saccade. Localization error was calculated as the difference between the horizontal position of the mouse click and the position where the bar was presented on the screen. Negative values indicate that the subject reported the perceived bar position to the left of the veridical bar position. This corresponds to a shift in the direction of adaptation.

The left panel of Figure 5A shows localization errors for flashed bars in a reactive saccade adaptation session of the subject of Figure 3. Each dot is the measurement from a single trial. The dots on the left present pre-adaptation measurements from the pre-adaptation target-off trials. The localization errors are small with a median at 0.4 deg, illustrating that localization was nearly correct before adaptation. The dots on the right are localization errors measured after adaptation in the post-adaptation target-off trials. These localization errors are shifted into the direction of adaptation with a median at -1.9 deg. A one-sided t-test revealed a significant difference between pre-adaptation and post-adaptation localization (t-test, $p < 0.01$).

The right panel of Figure 5A shows localization errors of the same subject in the reactive saccade adaptation session with stationary bars. These bars were continuously visible from trial start onwards and were turned off only when the eye tracker

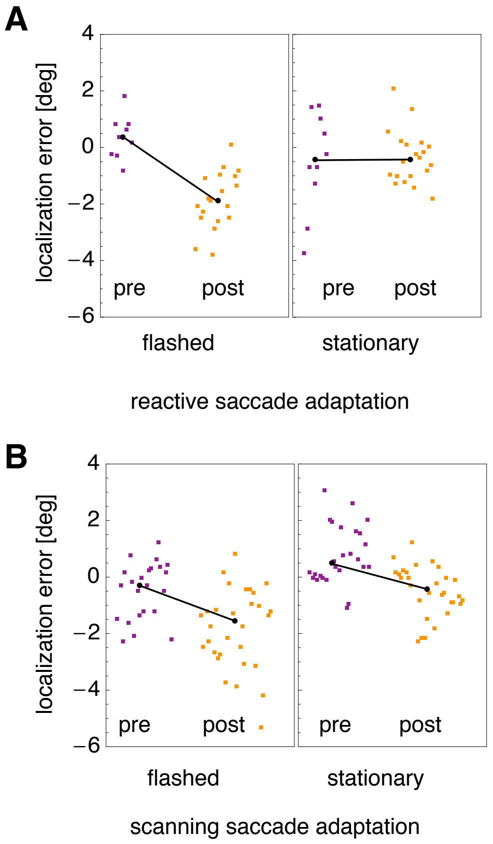

Figure 5: Examples of localization results from the subject of Fig 4. The localization error plotted on the ordinate is the difference between true and perceived location of a probe stimulus. Each point is data from a single trial. Trials are arranged in the order in which they were conducted. In each sub-figure, pre-adaptation data are plotted on the left, post-adaptation data on the right. The black line connects the medians of both data sets. A: localization results for reactive saccade adaptation with flashed (left) and stationary (right) probes. B: results for scanning saccade adaptation. Note that the data from this subjects was recorded in two adaptation sessions and that the combined data from both sessions is shown.

detected the onset of the saccade. Evidently, the localization of stationary bars was little affected by the adaptation of reactive saccades in this subject. The median localization error before adaptation was -0.5 deg, and the same median localization error was found after adaptation. Reactive saccade adaptation in this subject, therefore, only influenced the localization of flashed bars (Figure 5A, left panel), which were mislocalized in direction of adaptation, but not of stationary bars (Figure 5A, right panel).

Figure 5B presents localization data from the scanning saccade adaptation sessions. In these sessions the subject had to scan across four continuously visible targets at a voluntary pace, and the last saccade of that scanpath was adapted. The left panel of Figures 5B presents data obtained with flashed targets. In the pre-adaptation trials, localization errors were near 0 deg, with a median at -0.3 deg. In the post-adaptation trials, localization errors for flashed bars shifted significantly in the direction of adaptation (t-test, $p < 0.01$). Median localization error was at -1.6 deg. The right panel of Figure 5B shows localization errors for stationary bars. Median localization error before adaptation was 0.5 deg. In the post-adaptation trials, localization error for stationary bars were significantly (t-test, $p < 0.01$) shifted into the direction of adaptation with a median at -0.4 deg. Thus, scanning saccade adaptation influenced both the localization of flashed and the localization of stationary bars.

To quantify the adaptation-induced mislocalization in each condition, we took the difference between the median localization errors before and after adaptation in the direction of the adaptation. For the data of Figure 5 the mislocalization values were 2.3 deg for reactive saccade adaptation and flashed bars, 0 for reactive saccade adaptation and stationary bars, 2.5 deg for scanning saccade adaptation and flashed bars, and 1.6 deg for scanning saccade adaptation and stationary bars. Figure 6 shows the adaptation-induced mislocalization averaged across all subjects. After adaptation of reactive saccades (Figure 6A), flashed bars were mislocalized by 1.8 deg in the direction of saccade adaptation. There was no mislocalization for stationary bars. After scanning saccades were adapted (Figure 6B), flashed bars were mislocalized by 1.8 deg in the direction of adaptation. Stationary bars were mislocalized by 1.4 deg in the direction of adaptation. A two-way repeated measures ANOVA revealed a significant effect of the probe type (flashed or stationary, $F = 11.13$, $p < 0.05$), and a significant interaction between probe type and saccade type ($F = 7$, $p < 0.05$). We conclude that reactive saccade adaptation induces mislocalization for flashed but not for stationary probes, whereas scanning saccade adaptation induces mislocalization for both flashed and stationary probes.

It seems possible that saccade amplitudes are also influenced by the probes, and flashed and stationary probes could have differential influences on amplitudes which then might have differential effects on mislocalization. We have therefore analyzed how the appearence of the bar influenced the saccade amplitudes: For every subject we calculated the difference between the median amplitudes of the last 10 adaptation trials before a localization phase and the median amplitudes in the localization phase. This quantifies how much the appearance of the probes changed the amplitude of the saccades. Averaged over all subjects the appearance of the bars increased saccade amplitudes by about 1 deg. However, this influence of bar appearance on saccade amplitudes was equal across conditions and there were no significant differences between session types. An influence of the probes on the saccade amplitude can therefore not explain the different mislocalization effects.

The adaptation-induced mislocalization for flashed targets after reactive saccade adaptation is consistent with several earlier studies that found similar effects (Awater

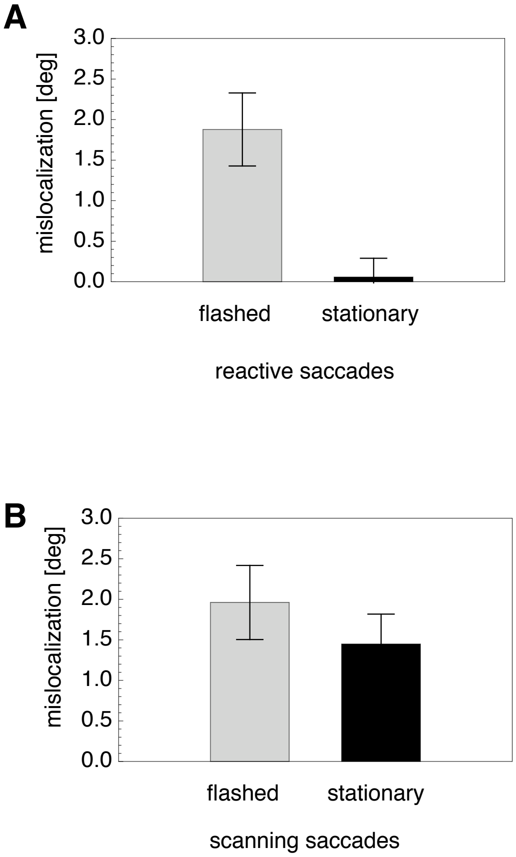

Figure 6: Average mislocalization after saccade adaptation. Plotted on the ordinate is the difference between the localization before and after adaptation. A: mislocalization of flashed (left) and stationary (right) probes after reactive saccade adaptation. B: mislocalization of flashed (left) and stationary (right) probes after scanning saccade adaptation. All data is from trials in which the saccade target was turned off during execution of the saccade (target-off trials). Error bars are standard errors.

et al., 2005; Bruno and Morrone, 2007; Georg and Lappe, 2009). Mislocalization of flashed probes after scanning saccades has not been tested previously, but adaptation of saccades in an overlap paradigm, which is usually considered to induce voluntary saccades, also induced mislocalization of flashed targets (Collins et al., 2007). The adaptation-induced mislocalization of stationary targets is a novel finding. Our observation that mislocalization of stationary targets occurs only after adaptation of scanning saccades, and not after adaptation of reactive saccades, suggests that the origin of this mislocalization is confined to the scanning saccade pathway. Since, mislocalization of flashed targets occurs for both saccade types, it may originate from mechanism that are shared between both pathways.

The flashed targets that we used as probe stimuli were intended to mimic the temporal properties of the typical targets of reactive saccades. In a reactive saccade trial, the saccade target suddenly appeared, like the flashed probes, but unlike the flashed probes the saccade target thereafter stayed on for the entire saccadic reaction time. To check whether the results obtained with flashed targets are also pertinent to appearing targets, we ran a control study with reactive saccade adaptation and bars that suddenly appeared 50 ms before saccade target onset and disappeared when a saccade was detected. Hence they stayed visible throught the saccadic reaction time. We tested two subjects (one of them the subject of Figure 5). Mislocalization with the appearing targets was the same as in the flashed bar condition in a reactive saccade adaptation session. We are therefore confident that our flashed target condition captures the essential properties of saccade targets that trigger reactive saccades.

The selectivity of the mislocalization for target types (flashed vs stationary) is reminiscent of the asymmetry often observed in the transfer of adaptation between saccade types. Adaptation transfers little from reactive saccades elicited by flashed targets to scanning saccades directed to stationary targets (Deubel, 1995; Fujita et al., 2002; Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2007). Similarly, mislocalization after reactive saccade adaptation occurs for flashed targets but not for stationary targets. Adaptation of voluntary saccades to stationary targets has been reported to transfer well to reactive saccades elicited by flashed targets (Deubel, 1995; Fujita et al., 2002; Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2007). Similarly, mislocalization after scanning saccade adaptation occurs for stationary targets and also for flashed targets. Reactive saccade adaptation thus influences saccades to and localization of flashed targets. Scanning saccade adaptation influences saccades to and localization of flashed and stationary targets.

The selectivity of the mislocalization for target types is also consistent with studies that measured influences of saccadic adaptation on hand-pointing movements. Cotti et al. (2007) adapted reactive and scanning saccades in different sessions and studied the respective effect on hand pointing to stationary targets. Pointing changed in the direction of adaptation only after the adaptation of voluntary saccades. There was no effect after the adaptation of reactive saccades. Since they used stationary pointing targets, their result is consistent with our mislocalization, which, for stationary targets was found only after adaptation of scanning but not after adaptation of reactive saccades. Bruno and Morrone (2007) adapted reactive saccades and asked subjects to indicate the location of flashed bars with a hand reaching movement after execution of the saccade. They found that reaching end points changed in the direction of adaptation. The change in the reaching movement was similar to the perceptual mislocalization of the bar reported verbally. Their results are consistent with our data since they used flashed targets after adaptation of reactive saccades. We therefore conclude that effects of saccade adaptation on visual localization de-

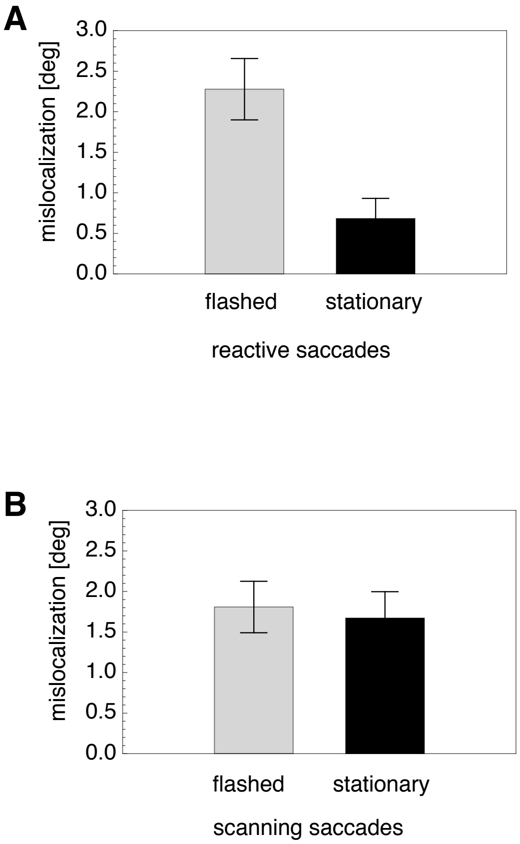

Figure 7: Average mislocalization after saccade adaptation in trials in which the saccade target was visible after saccade offset (target-on trials). Same conventions as in Figure 6.

pend on the kind of saccade that is adapted and the properties of the localization stimulus, but can be measured similarly in perceptual and hand motor tasks.

2.3.3 Localization results in the target-on and transfer conditions

For the above analysis, we have used only data from target-off trials in order to avoid any interference of visual reference information from the view of the post-saccadic target. A similar analysis of the target-on trials gave localization results very similar to those of the target-off trials (Figure 7). After reactive saccade adaptation, flashed bars were mislocalized by 2.3 deg, and stationary bars were mislocalized by 0.7 deg. After scanning saccade adaptation, flashed bars were mislocalized by 1.8 deg, and stationary bars were mislocalized by 1.7 deg. A two-way repeated measures ANOVA revealed a significant main effect of probe type, ($F = 10.24$, $p < 0.05$)

and a significant interaction between the probe type and saccade type, ($F = 16.55$, $p < 0.01$).

Overall, mislocalization in the target-on condition was slightly higher than in the target-off condition. The differences were small (about 0.3 deg), and did not reach significance (t-test, $p = 0.06$). We conclude that post-saccadic visual references from the target location contribute only little to the mislocalization effect. This is consistent with earlier observations with reactive saccades and flashed probes in which target-on and target-off trials gave similar mislocalization (Awater et al., 2005). Collins et al. (2007), on the other hand, observed differences in mislocalization of flashed targets between target-on and target-off conditions with overlap saccades. However, these differences were most pronounced for probe locations further away from the saccade target, and were only small in the vicinity of the saccade target where the measurements in our study were taken.

We also measured mislocalization in the transfer trials. In these trials, one type of saccade was adapted, but the other type of saccade was performed. Because adaptation transfer was only partial (Figure 4) the amplitudes of saccades in the transfer trials were typically less adapted than when the same saccades were performed after genuine adaptation. Figure 8A shows mislocalization when reactive saccades were performed after scanning saccades had been adapted. Mislocalization was 0.6 deg for flashed bars and 0.1 deg for stationary bars.

Mislocalization when scanning saccades were performed after reactive saccades had been adapted was 0.6 deg for flashed bars and 0.3 deg for stationary bars (Figure 8B). There was no significant difference between the conditions, but the average mislocalization in the transfer trials was significantly different from zero (t-test, $p < 0.01$). Yet, a comparison with Figure 6 reveals that the amount of mislocalization is overall lower in the transfer trials. This is consistent with the amplitudes of the transfer saccades being only weakly adapted. It shows that not only the type of saccade that is adapted influences the mislocalization but also the type of saccade that is prepared.

In summary, we conclude that adaptation both of reactive and of scanning saccades influences the localization of visual stimuli, and that this influence depends on whether the stimulus is flashed or stationary. After adaptation of reactive saccades localization of flashed bars was shifted into the direction of adaptation as observed in earlier studies (Georg and Lappe, 2009; Awater et al., 2005). The localization of stationary bars however was unaffected by reactive saccade adaptation. After adaptation of scanning saccades, in contrast, both flashed and stationary bars were mislocalized into the direction of saccade adaptation. The magnitude of mislocalization depends on the amount of adaptation, since in the transfer trials, in which the

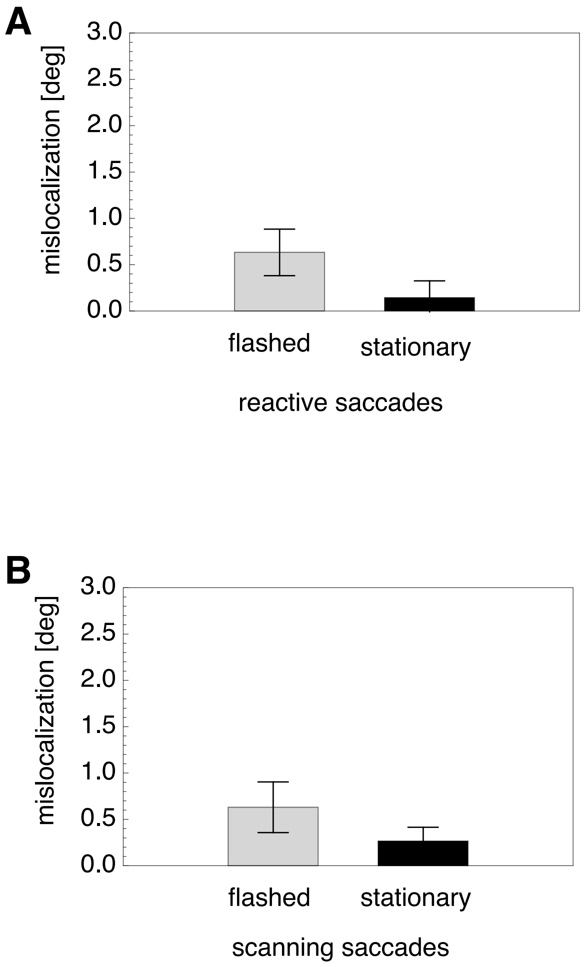

Figure 8: Average mislocalization in the transfer-test trials. A: mislocalization when reactive saccades were performed after adaptation of scanning saccades. B: mislocalization when scanning saccades were performed after adaptation of reactive saccades. In all cases the saccade target was turned off during execution of the saccade. Error bars are standard errors.

amount of adaptation was reduced, mislocalization was also smaller.

2.4 Discussion

To explain the different influences of reactive and scanning saccade adaptation on the localization of flashed and stationary targets, we must discuss the possibilities by which the visual system may estimate the location of the targets. The bars in our study were presented before the execution of the saccade. Thus, the position of the bar had to be encoded before the saccade, then retained in transsaccadic memory, and later retrieved after the saccade ended. For such trans-saccadic localization, the visual system might encode objects with respect to visual landmarks, such as the saccade target, and retrieve them after the saccade from visual information about the post-saccadic location of the saccade target (McConkie and Currie, 1996; Deubel et al., 1996, 2002; Awater and Lappe, 2006). In this case, when the saccade target steps back during saccade execution, the objects that are referenced to it would step back, too, thus inducing a trans-saccadic mislocalization. However, in the target-off trials, on which we based our main analysis, the target was not visible after the saccade, and could not have served as a landmark for retrieval. Thus, visual reference information cannot explain the mislocalization. However, a small difference between the target-on and the target-off conditions was noticeable. Thus, visual reference information from the target back-step might contribute to the amount of mislocalization, depending on conditions. An influence of the visual target back-step has also been reported by (Collins et al., 2007), who showed that the spatial pattern of mislocalization for positions further away from the saccade target depended on the presence or absence of the target after the saccade. However, the main effect of adaptation-induced mislocalization cannot originate from visual references of the saccade target since it was measured in the target-off trials.

In the absence of the saccade target, the visual system may instead use the current gaze direction as reference for the retrieval from trans-saccadic memory. In this scenario, the stimulus is again encoded relative to the saccade target position. After the saccade, the position of the bar is retrieved relative to the post-saccadic gaze direction. Because the post-saccadic gaze direction after an adapted saccade is different from that after a normal saccade, the reported location should be shifted in the direction of adaptation. However, in this scenario the amount of mislocalization should be the same as the amount of adaptation. Since in our study (and in several others (Georg and Lappe, 2009; Collins et al., 2007; Awater et al., 2005)) the amount of mislocalization was much smaller than the amount of adaptation this scenario is unlikely.

A further possibility for trans-saccadic mislocalization is the remapping of spatial location based on an efference copy signal. An efference copy of the saccade motor command may be used to predict the post-saccadic location of the object based on its pre-saccadic location and the amplitude of the saccade. Mislocalization may then arise if the efference copy signal does not match the amplitude of the saccade. This might occur if the efference copy reflects the size of the unadapted saccade, e.g. if adaptation takes place in a neural structure that is downstream from the structure that generates the efference copy. If this were the case, the pre-saccadic location would be remapped to a post-saccadic location as if the saccade were unadapted. Since the saccade is actually shorter, a mislocation in the direction of the saccade would be the consequence (Bahcall and Kowler, 1999; Hernandez et al., 2008). However, the unadapted efference copy explanation would predict the same amount of mislocalization for all saccade and stimulus types. Our results show that this is not the case: first, the amount of mislocalization for flashed and stationary bars is clearly different after reactive saccade adaptation. Second, the mislocalization of stationary bars is different after reactive and after scanning adaptation. One may salvage the efference copy explanation by postulating different efference copy signals for different saccade types. The efference copy of reactive saccades would remap flashed objects, while the efference copy for scanning saccades would remap both flashed and stationary objects. Such a concept of multiple efference copies is not unrealistic since many brain structures take part in saccade generation, and the difference between reactive and voluntary saccade adaptation already indicates partially separate pathways. However, if the efference copy for reactive saccades remaps only flashed, but not stationary targets, during normal reactive saccades, stationary objects should appear perceptually unstable, which is clearly not the case. The efference copy explanation is also inconsistent with the spatial pattern of mislocalization reported by Collins et al. (2007). Their data indicated that mislocalization for objects further away from the saccade target is not correlated with the performed saccade, i.e., the saccade for which the efference copy signal is generated, but with the adaptation state for the saccade that would be required to reach the object, even when this saccade is not performed.

According to the above considerations neither post-saccadic reference signals nor efference copy or eye position signals can explain the dependence of the mislocalization on the target properties. We must therefore consider differences between the processing of the flashed and the stationary targets in the pre-saccadic encoding or memory stages. One possibility is that the mechanism of adaptation includes a modification of target location at an early stage of the sensorimotor transformation, and that this modified target location is used for the trans-saccadic memory. If this were the case, visual localization and saccade targeting would be equivalent in the sense that the perceived location of an object is derived from the target metrics of the saccade that would be needed to acquire the object (Collins et al., 2007). Thus, saccade metrics would be used for saccade targeting and visual localization alike. If saccade adaptation involves a change to the saccade target metrics, the perceived location of the object at the target location must change in a similar fashion. In this view, if the pathways that generate the saccade differ for different target conditions (flashed vs. stationary), the localization should also differ and depend on the target properties.

This proposal predicts that part of the adaptation of the saccade amplitude stems from the remapping of target location rather than from the adjustment of motor execution. Some evidence for an involvement of target remapping in saccadic adaptation is reported in a few recent studies. Ethier et al. (2008a) have analyzed the temporal velocity profile of adapted saccades and compared it to predictions of a model that can adjust saccade amplitude either by adjusting the parameters of the forward model of the saccade generator or by adjusting the target signal (Chen-Harris et al., 2008). The comparison showed evidence for adjustment of both motor and target parameters, although the target parameter adjustment was necessary only for gain increasing saccades. A computational model by Gancarz and Grossberg (1999) had earlier suggested that a component of target remapping is needed to explain the selective adaptation of scanning saccades. Other evidence that saccade adaptation may include changes in target localization stages in addition to changes in motor execution comes from recent studies of transfer of adaptation between saccades and anti-saccades (Cotti et al., 2009; Collins et al., 2008; Panouilleres et al., 2008). In these studies, amplitudes of normal saccades in one direction were adapted, and it was then measured how much change of saccade amplitude occured for anti-saccades in the same, and in the opposite direction. Specifically anti-saccades in the opposite direction provide an indication of adaptation in the target localization stage because these anti-saccades are instructed by the same target as the normal saccade but are executed in the opposite direction. Adaptation in the motor stage of saccade execution should, therefore, not have an effect on these saccades. Cotti et al. (2009) compared anti-saccade transfer for gain decreasing reactive and scanning saccades. They found transfer consistent with changes in target localization for scanning saccades but not for reactive saccades. Collins et al. (2008) found no transfer for anti-saccades in the opposite direction in the overlap paradigm. Panouilleres et al. (2008) adapted reactive saccades and found, in some subjects, transfer to opposite anti-saccades for gain increasing but not for gain decreasing adaptation. Taken together, these studies do not unambiguously show that saccade adaptation always involves a component of target localization adjustment, but they indicate that target adjustment can occur, depending on conditions and subjects.

Adaptation in target localization stages is also supported by the finding that hand pointing movements to a continously presented target were misdirected after voluntary saccade adaptation but not after reactive saccade adaptation (Cotti et al., 2007). This is consistent with our data since we also found mislocalization for stationary bars only after adaptation of voluntary saccades. However, we also found that reactive saccade adaptation affects the localization of flashed bars. Evidence that reactive saccade adaptation affects localization via hand pointing movements for flashed bars comes from Bruno and Morrone (2007).

However, if mislocalizations were the result of a simple modification of early stage of the sensorimotor transformation then this modification should be revealed whatever the type of saccade being prepared. In the transfer-test trials, however, localization is also a function of the type of saccade that is prepared, not only the type of saccade that is adapted. In addition, one might expect that a modification of early stage of the sensorimotor transformation should also lead to a mislocalization in case the saccade is not performed. Previous studies, in contrast, found no mislocalization during fixation (Awater et al., 2005; Collins et al., 2007). However, if the mislocalization results from modifications in the pre-saccadic encoding or memory stages of trans-saccadic memory, it must not necessarily appear also during fixation, since in this situation trans-saccadic memory is not involved. To reconcile such a trans-saccadic memory explanation with the results from the transfer-test trials, one would have to assume that trans-saccadic memory draws on sensorimotor representations which are specific to the saccade that is currently prepared, mainly process particular types of stimuli, i.e. flashed or stationary and may be modified by saccadic adaptation

This explanation is quite speculative and should be treated cautiously, but in essence it predicts that trans-saccadic memory is formed not as a visual buffer but as a buffer constructed from the activities in brain areas that are already involved in saccade planning and preparation.

The difference between the mislocalization of flashed and stationary targets may also relate to different coordinate frames in which saccades are planned. Niemeier et al. (2003) proposed that reactive saccade are coded in eye-centered coordinates whereas voluntary saccades are coded in head-centered coordinates. Different coordinate systems could explain the present data assuming that stationary targets always are coded in head-centered coordinates and thus mislocalized for adapted scanning saccades only whereas flashed targets might be coded in different coordinates.

3 Study II: Localization of targets during fixation

3.1 Introduction

Visual localization provides the basis for coordinate behavior. Sensorimotor theories of vision claim dependencies between visual and action maps or in a stronger sense common representations for vision and action (O'Regan and Noe, 2001).

Systematically modifying the contingencies between sensory and motor maps with, for instance, prism adaptation can restructure visual perception of space. Visual perception on the other hand can be substituted by learning the contingencies between external objects and tactile stimulation (Bach y Rita, 2004). In the present study we want to approach the question whether visual localization and saccade metrics share a common representation. We therefore modify saccade metrics with the saccade adaptation paradigm. An adaptive shortening or lengthening of saccade amplitudes can be induced by a successive displacement of the saccade target (McLaughlin, 1967). Saccade adaptation relies strongly on cortical mechanisms (Desmurget et al., 1998; Robinson and Fuchs, 2001; Catz et al., 2008; Golla et al., 2008) and therefore affects the localization of visual targets (Awater et al., 2005; Collins, 2007; Georg and Lappe, 2009). However, up to now no adaptation-induced mislocalization during fixation could be found.

Studies suggest that inward and outward adaptation are achieved by different mechanisms. A computational model by Ethier et al. (2008b) indicates that outward adaptation is achieved by an internal remapping of the saccade target position and inward adaptation by a feedforward learning based on movement errors. Other experimental evidences also suggest that outward adaptation induces changes in the saccade target localization stage (Cotti et al., 2009; Collins et al., 2008; Panouilleres et al., 2008). Hand-pointing movements to the location of the saccade target were misdirected after outward but not inward adaptation.

We tested whether saccadic adapation also modifies visual localization during fixation. In contrast to previous studies, which did not find mislocalization during fixation (Awater et al., 2005; Collins, 2007; Georg and Lappe, 2009), our experiments were conducted in the absence of any visual landmarks and separately for inward and outward adaptation. We found strong mislocalization after outward adaptation, but only a small effect after inward adaptation. An analysis of saccadic velocity profiles indicated that outward, but not inward adaptation was consistent with a change of the saccade target representation. A second experiment used a novel saccade adaptation method which applies a constant postsaccadic visual error. Analysis of velocity profiles suggested that this method evoked target remapping for both inward and outward adaptation. With this method, we found mislocalization after both inward and outward adaptation as a function of visual error size. We conclude that changes in saccade metrics are accompanied by changes in visual localization behavior, thus emphasizing the importance of saccade vectors for the representation of space.

3.2 Methods

3.2.1 Saccade Trials

At trial onset a fixation point (0.75 x 0.75 deg) appeared at a horizontal position 10 deg to the left of the central position. The vertical position varied from trial to trial and was a randomly assigned value between 10 deg above and 10 deg below the screen center. This method is preventing fatigue effects due to a monotonous setup. The subject was instructed to direct gaze on the fixation point. The fixation point was presented for 800 ms plus a randomly chosen period between 0 and 300 ms. Simultaneously with offset of the fixation point a saccade target (0.75 x 0.75 deg) appeared 13 deg to the right of the fixation point. The subject is supposed to perform a saccade to the target as soon as possible. The trial ended 830 ms after saccade target onset and the next trial started automatically.

3.2.2 Saccade Adaptation

Saccade adaptation was induced with two different methods. In the normal saccade adaptation method the saccade target was displaced when the eye-tracker detected the gaze position to be more than 2.5 deg rightward of the fixation point. With this method we induced inward and outward adaptation with a 3 deg target displacement.

In the constant visual error adaptation a method was used which first used by Robinson et al. (2003). In this method the saccade landing position is predicted online. The saccade target is diplaced with a constant degree relative to the predicted landing position of the saccade. To predict the saccade landing position a velocity criterion was used. Gaze position was sampled with 1000 Hz. On the basis of the gaze position data saccade velocity was calculated online. When the velocity came under a predetermined threshold of 30 deg/sec, gaze position was taken as the prediction of the saccade landing point. This method displaces the saccade target at the end of the saccade, which however is not critical since adaptation can be induced with a target movement maximally 80 ms after saccade end (Fujita et al., 2002). The mean error of the landing point prediction was 0.01 deg. With this method six different constant visual errors were applied in separate sessions, (-1, -2 and -3 deg) for inward adaptation and (1, 2 and 3 deg) for outward adaptation.

3.2.3 Localization Trials

Localization was tested in a block of trials before adaptation and in 5 blocks of trials interleaved in the course of adaptation. Each block contained 20 localization trials. During the fixation trials no fixation point or any other visual cue were present. Subjects were instructed to direct gaze at the center of the screen and avoid any eye movement during the entire block of localization trials. When ready, the subject had to press the space button on the keyboard to start a trial. The eyetracker sampled gaze position online. 30 ms after the subject pressed the space button a small bar (0.2 x 3 deg) appeared 13 deg to the right of the subjects current gaze position. The bar was flashed for 30 ms. 1000 ms after bar offset a mouse pointer appeared on the right border of the screen. The mouse pointer appeared at the bottom border of the screen and a randomly chosen horizontal position between 35 deg and 40 deg. The subject was instructed to indicate the perceived position of the bar by pressing the mouse button. After the mouse button was pressed the mouse pointer disappeared and the subject could start the next trial with the space button. The localization error was calculated as the deviation of the mouse click position from the position where the bar was presented. Subjects were instructed to click in the right corner of the screen in case they did not perceive the bar. Localization trials were discarded from analysis when subjects clicked in the right corner or a saccade was detected. In total, 12 % of all localization trials were discarded.

3.2.4 Mimic adaptation

To analyze, whether saccade adaptation induced changes in peak velocities can be found, sessions were run, which allowed to compare peak velocities of adapted saccades with peak velocities of unadapted saccades with the same amplitude size. Since saccade velocities depend on saccade amplitudes we chose saccade amplitudes from the adaptation sessions and used them to determine saccade target position in the mimic trials. In mimic adaptation sessions the trial sequence was the same as in adaptation sessions with the only difference that no target displacement was applied. Mimic adaptation sessions were run for every adaptation session. We could then compare saccade characteristics from the adaptation trials with the mimic trials. In the analysis we compared saccade amplitude of each trial from the adaptation sesssion with saccade amplitude of the same trial from the mimic adaptation session. We analysed all trials in which saccade amplitudes in the adaptation condition did not differ more than 0.5 deg from the mimic condition. The comparison was accomplished for standard adaptation data and for data of a 3 deg constant error condition.

3.2.5 Trial Sequence

The trial sequence was the same in all experiments. An experiment started with 20 localization trials. These were followed by 20 pre-adaptation trials. During the pre-adaptation trials the saccade target remained in its initial position. Every 40 trials a white screen was presented for 4 sec. The white screen served as a rest and prevented dark adaptation. After trial 39 saccade adaptation trials started. Here, the saccade target was displaced with one of the methods described above. In the course of adaptation, blocks of localization trials (each 20 trials) were interleaved every 200 adaptation trials (trials: 240-260, 460-480, 680-700, 900-920, 1120-1140).

3.2.6 Setup

All experiments were conducted in complete darkness to avoid the influence of any visual landmarks. The subject was seated 57 cm in front of a 22" computer monitor (Eizo FlexScan F930) with the head stabilized by a chin rest. The visible screen diagonal was 20", resulting in a visual field of 40 deg x 30 deg. Stimuli were presented on the monitor with a vertical frequency of 120 Hz at a resolution of 800 x 600 pixels. The room was completely dark. To avoid visibility of the screen borders the display monitor was covered with a transparent foil that reduced the luminance by about 2 log units. Eye movements were monitored by the Eyelink 1000 system (SR Research, Ltd., Canada), which samples gaze positions with a frequency of 1000 Hz. Viewing was binocular but only the dominant eye was recorded. 5 subjects (4 female, 1 male, mean age: 25) participated in the inward adaptation experiments. 5 different subjects (4 female, 1 male, mean age: 28) participated in the outward adaptation experiments. The order of conditions was counterbalanced across subjects. For every subject a break of at least 48 h was interposed between successive sessions. For outward adaptation with a 3 deg constant visual error only 4 subjects were measured in the mimic adaptation condition. In this conditon only data from 4 subjects were compared.

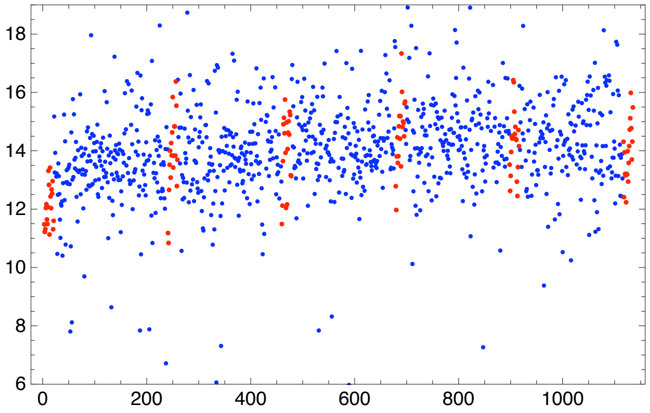

Figure 9: Trial structure for a single outward adaptation session. Red points represent perceived positions of the probe bars relative to gaze positions. Blue points depict saccade amplitudes. In the pre-adaptation trials the saccade target was shown at 13 deg and was displaced 3 deg outwards when the saccade was in-flight.

3.3 Results

3.3.1 Normal adaptation method

An example adaptation session is shown in Fig 9. The session started with 20 localization trials. The probe bar was presented 13 deg to the right of the measured gaze direction. The red points indicate where the subjects reported the perceived bars relative to gaze directions. Localization in these first 20 localization trials was slightly shifted in the direction of the fovea with a median of 12.1 deg. Foveal shifts during fixational localization have been reported earlier (Müsseler et al., 1999). In trials 20 - 40 a saccade target was shown at 13 deg. To obtain a pre-adaptation measure of saccade amplitudes the target did not jump during the saccade in these trials. The median saccade amplitude was 12.5 deg in the pre-adaptation trials thus showing a typical saccade undershoot. From trial 40 on the saccade target jumped 3 deg outwards during execution of the saccade to induce saccade adaptation. After 1000 trials saccade amplitudes reached 13.8 deg.

Localization was measured in 20 pre-adaptation trials and during the course of adaptation in 5 phases, each consisting of 20 trials. Localization error was calculated as the difference between the horizontal position of the mouse click and the position where the bar was presented on the screen. We calculated mislocalization as the difference between median localization error of the pre-adaptation trials and median localization error of each of the 5 phases during adaptation. To estimate the amount of adaptation we compared saccade amplitudes of the pre-trials with saccade amplitudes at the time when localization was tested. Since the adaptation state might change during the localization phase we calculated the median over amplitudes from

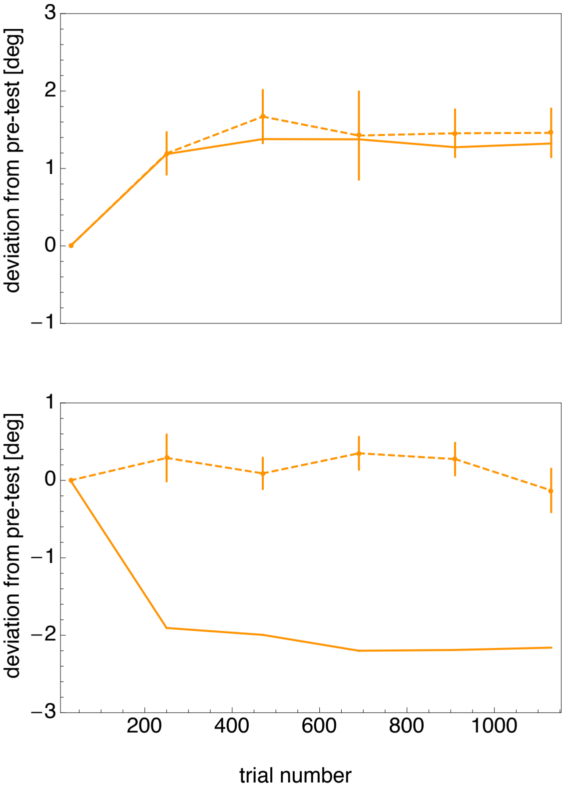

Figure 10: Mean mislocalization (dashed line) and mean adaptation (solid line) averaged over all subjects. The upper panel shows results from outward adaptation sessions and the lower panel shows results from inward adaptation sessions. Error bars are standard errors.

the last ten trials before a localization phase and the following ten trials after the specific localization phase. Fig 10 shows the amount of adaptation (solid line) and the amount of mislocalization (dashed line) after every 200 trials averaged over all subjects.

Results from outward adaptation are shown in the upper panel. Outward adaptation reached a maximal amplitude increase of 1.4 deg. The 3 deg outward target displacement therefore induced an adaptation of 46 %. The amount of mislocalization shows a very similar development and increases with the same size as the adaptation. After 1000 trials of adaptation probe bars were mislocalized 1.3 deg in the direction of adaptation. Results from inward adaptation are shown in the lower panel. A strong amplitude decrease can be seen. The maximal amount of inward adaptation was -2.2 deg, which was 73 % of the 3 deg target displacement. Mislocalization amount after inward adaptation is strikingly different than after outward adaptation. Mean mislocalization from all 5 localization phases was around zero.

Not until about 1000 trials a marginal trend of mislocalization in the direction of adaptation can be seen.

For outward adaptation a one way repeated measures ANOVA confirmed a significant increase in mislocalization in 4 phases during adaptation compared to mislocalization measured before adaptation, ($F = 7.425$, $p = 0.016$). Only mislocalization after 600 trials marginally failed to reach significance. For inward adaptation no significant difference between mislocalization during adaptation and the pre-test values was revealed ($F = 1.004$, $p = 0.422$).

In order to estimate whether adaptation was based on target remapping or feedback mechanisms we compared velocity profiles from the adaptation and the mimic adaptation sessions. The mimic adaptation sessions were designed to evoke the same amplitude sizes in the same trial order as in the adaptation sessions. We calculated for each subject the mean peak velocities separately for adaptation and mimic sessions of the last 120 adaptation trials.

Mean peak velocity in inward adaptation sessions was 333 deg/sec. In the according mimic sessions peak velocity was 364 deg/sec. The difference was statistically significant (paired t-test, $p = 0.014$). Mean peak velocity in outward adaptation sessions was 477 deg/sec. In the according mimic sessions peak velocity was 457 deg/sec. The difference was not statistically significant (paired t-test, $p = 0.237$).

Saccade adaptation in the outward paradigm was slower and and less complete than inward adaptation. This result has also been observed in other studies (Noto et al., 1999; Bahcall and Kowler, 1999; Robinson et al., 2003). We wondered whether the different mislocalization after outward and inward adaptation might be due to the different adaptation characteristics. In summary, after outward adaptation with the normal adaptation method mislocalization was found which was as strong as the amount of adaptation. However, no mislocalization was found after inward adaptation. The amount of adaptation was higher in the inward than in outward adaptation. To explain the differences between outward and inward adaptation we analyzed the saccade velocity profile by comparing peak velocities of adapted saccades with peak velocities of unadapted saccades of the same amplitude size. We found that in our setup inward but not outward adaptation is accompanied by a modification of saccade peak velocities. This finding is consistent with a model prediction of Ethier et al. (2008b) and might indicate that outward adaptation is based on a modification of the internal saccade target position and inward adaptation is achieved by a change in the motor command.

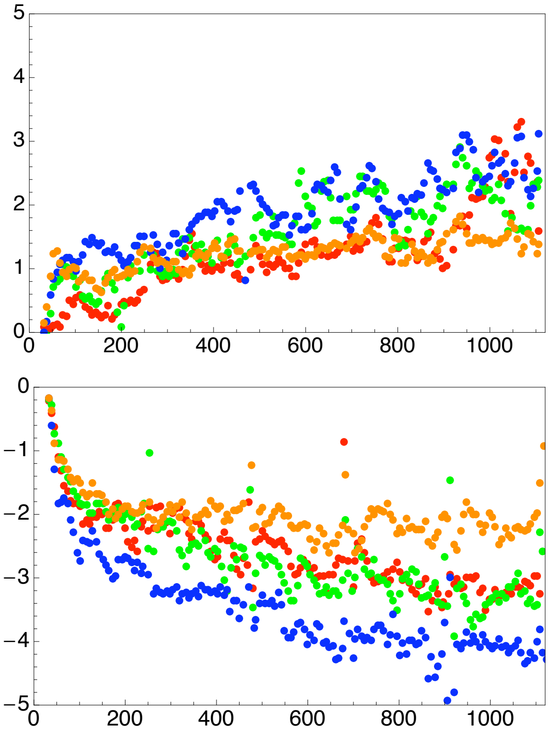

Figure 11: Mean curves from adaptation with the constant visual error method. Results are shown for adaptation with 1 deg visual error (red), 2 deg visual error (green) and 3 deg visual error (blue). Mean curves from adaptation with the normal adaptation method are shown in orange. The upper panel shows curves from outward adaptation sessions and the lower panel shows results from inward adaptation sessions.

3.3.2 Constant visual error adaptation method

To test the dependence of mislocalization from the postsaccadic visual error we induced saccade adaptation with the constant visual error method as described in the methods part. Fig 11 shows adaptation curves, which were measured with the constant visual error method. For both, inward and outward adaptation we used three different constant visual errors in separate sessions. Fig 11 shows mean curves from adaptation with the constant visual error method averaged over all subjects. We induced adaptation with a constant visual error of 1 deg (red curve), 2 deg (green curve) and 3 deg (blue curve). To compare the constant visual error adaptation method with the normal adaptation method we also plotted the curve from the normal adaptation method (orange curve). In both, inward and outward constant visual error adaptation the amount of adaptation depended on the visual error size. In inward adaptation for instance amplitude decrease is strongest for adaptation with 3 deg constant visual error. After 1000 trials every constant visual error condition produced a stronger adaptation than the normal method.

Fig 12 shows the mislocalization results after adaptation with constant visual er-

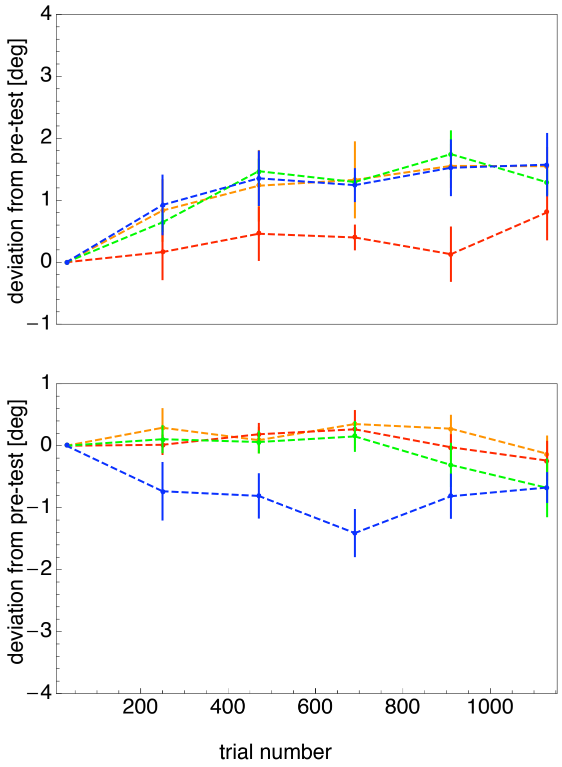

Figure 12: Mean mislocalization results averaged over all subjects. Results are shown for mislocalization after adaptation with 1 deg visual error (red), 2 deg visual error (green) and 3 deg visual error (blue). The upper panel shows curves from outward adaptation sessions and the lower panel shows results from inward adaptation sessions.

ror. Mislocalization results after outward adaptation are shown in the upper panel. Outward adaptation with the constant visual error method induced strong mislocalization in the direction of adaptation for 2 deg and 3 deg constant visual error. Mislocalization increased over the course of trials comparable to the increase in the size of saccade amplitudes. After 1000 trials mislocalization reached its maximum of 1.57 deg for the 3 deg constant visual error. Maximal mislocalization for the 2 deg constant visual error was 1.75 deg after 800 trials. Mislocalization measured after adaptation with a 1 deg constant visual error were scattered around zero deg, although a small increase after 1000 trials was observable with -0.8 deg of mislocalization.

The lower panel of Fig 12 shows mislocalization results after inward adaptation. The constant visual error method induced mislocalization for this condition, too. This was most noticeable for adaptation with a 3 deg constant visual error, where the maximal mislocalization of -1.41 deg was reached after 600 trials. Mislocalization after inward adaptation with 1 deg and 2 deg scattered around zero deg. Small amounts of mislocalization were observable after 1000 trials, -0.24 deg for 1 deg constant visual error and -0.68 for 2 deg constant visual error.

For outward adaptation with a constant visual error of 1 deg a one way repeated measures ANOVA showed that there was no significant mislocalization ($F = 1.358$, $p = 0.306$). For outward adaptation with a constant visual error of 2 deg a one way repeated measures ANOVA confirmed significant mislocalization for all 5 localization phases ($F = 13.203$, $p = 0.001$). Also in outward adaptation with a constant visual error of 3 deg significant mislocalization was revealed by a one way repeated measures ANOVA ($F = 5.501$, $p = 0.023$). After 400 trials all localization phases were significantly different from the pre-test phase.

For inward adaptation with a 1 deg constant visual error a one way repeated measures ANOVA showed that there was no significant difference between mislocalization during adaptation and the pre-test values ($F = 0.816$ $p = 0.484$). After inward adaptation with a 2 deg constant visual error a one way repeated measures ANOVA showed that mislocalization was not significantly different from pre-test, ($F = 1.876$, $p = 0.216$). After adaptation with a 3 deg constant visual error a one way repeated measures ANOVA showed that only mislocalization measured after 600 and after 1000 trials was significantly different from pre-test ($F = 2.079$, $p = 0.019$).

Mean peak velocity in inward adaptation sessions with a constant visual error of 3 deg was 344 deg/sec. In the according mimic sessions with a constant visual error of 3 deg peak velocity was 325 deg/sec. The difference was statistically significant (paired t-test, $p = 0.14$). Mean peak velocity in outward adaptation sessions was 446 deg/sec. In the according mimic sessions peak velocity was 475 deg/sec. The difference was not statistically significant (paired t-test, $p = 0.2$).

3.4 Discussion

We report mislocalization of visual targets after saccade adaptation. Magnitude and timecourse of mislocalization were highly comparable to the amplitude increase after outward adaptation. Localization was measured during fixation in complete darkness and since all landmarks were eliminated no visual references can explain the mislocalization results.

We found that the postsaccadic visual error, i.e. the discrepancy between the actual landing point and the saccade target, was the relevant factor inducing visual mislocalization. To isolate the influence of the visual error on perceptual effects we used an adaptation method where the visual error was kept constant. With a small constant visual error (1 deg) saccades adapt, but no mislocalization occurred. However, with constant visual errors of at least 2 deg visual targets were mislocalized. In the normal saccade adaptation paradigm the visual error depended on the timecourse of adaptation. Visual errors decrease during the course of adaptation. Therefore, the amount of mislocalization rose rapidly at the beginning of adaptation and then remained constant in later trials when visual errors were smaller. This is the result we obtained in the outward paradigm with the normal adaptation method. On the contrary, in the inward adaptation paradigm the visual error was reduced to 1 deg so fast that no mislocalization occurred. After inward adaptation with a constant visual error of 3 deg there was mislocalization. These results are consistent with earlier studies. Mislocalization for hand-pointing movements after outward adaptation has been reported by Hernandez (2008). Other studies tested visual localization during fixation after inward adaptation and found no or only small effects (Moidell and Bedell, 1988; Awater et al., 2005; Collins, 2007; Georg and Lappe, 2009).

In order to induce mislocalization, saccade adaptation has to interact with the visual localization mechanism. Recent evidence suggests that when adaptation occurs in the motor commands, modifications in the velocity profile are observable. We analyzed peak velocities of adapted saccades and compared them to unadapted saccades of the same amplitude size. Consistent with Ethier et al. (2008b) we found that inward adaptation significantly reduced saccade peak velocities. Outward adaptation, however, left peak velocities unchanged. This indicates that outward adaptation takes place at a target localization stage and is consistent with the existence of mislocalization after outward adaptation. Inward adaptation with the constant visual error method did not modify peak velocities. We therefore conclude that saccade adaptation induces mislocalization. The strength of the mislocalization depends on the size of the postsaccadic visual error. We propose that mislocalization is the result of a modification in the saccade target representation. Changes in the saccade metrics thus are followed by changes in visual localization. Therefore, the spatial organization of visual localization might be based upon saccade metrics.

4 Conclusion

We collected and analyzed data on the influence of motor and visual parameters on object localization obtained from two saccade adaptation studies. In these studies the question of transfer of fragments and the influence of motor parameter adaptation on fragment location were investigated.

The first study dealed with the fact, that saccade adaptation is paradigm specific. For different presentations of the targets, adaptation amounts are different. Furthermore, different amounts of transfer between these types can be found, where the transfer is a measure for the gain change of one saccade type after adaptation of another type. In the experiment scanning and reactive saccades were tested. Whereas reactive saccades elicit saccades to a suddenly appearing target, scanning saccades follow a set of targets, which can be planned before starting the trial. In the study, corresponding to the saccade paradigms localization targets were chosen to determine, if also fragment transfer from one retinotopic input to the next is target type specific. The localization targets were presented shortly before the saccade. For reactive saccades, a flashed target was used. This target appeared about 100 ms before the saccade started and lasted for 20 ms only. In contrast, in analogy to the stationary saccades a stationary bar was used, which appeared at the beginning of the trial and lasted until the saccade started. Indeed, a type specific transfer of adaptation to localization was found. When adapting reactive saccades, only flashed bars were mislocalized, whereas for scanning saccades stationary and flashed bars underwent mislocalization. As any dependency on visual references could be excluded, the first study reveals that saccade type dependent adaptation influences transfer of fragments depending on their nature.

The second study pursues the idea of mutual influence of metrics and broadens the manifestation of the influence of saccade metrics on fragment metrics by uncoupling it from the saccadic mechanisms. In this study mislocalization of fragments was tested in a fixation condition. It was found that the visual error after a saccade can be considered as the relevant factor. Two adaptation types were tested. They differ by the development of the visual error in the course of adaptation. Whereas in the classical paradigm the error goes exponentially to zero, in the second paradigm the error stays constant for each trial. In fact the fast reduction of error in the classical paradigm, especially for inward adaptation, prevented a mislocalization of fragments. For outward adaptation the error evolved parallel to the development of the visual error. This dependency was affirmed by the constant error paradigm, where the mislocalization depended on the error size. As soon as the error exceeded one degree, mislocalizations of the size of the adaptation evolved.

Finally, it can be concluded, that visual errors after saccades influence not only saccade metrics, but also the localization of fragments in a saccade situation as well as in a fixation condition.

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