Title: Differences in inter-saccadic adaptation transfer between inward and outward adaptation

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Abstract

Saccadic adaptation is a mechanism to increase or decrease the amplitude gain of subsequent saccades if a saccade is not on target. Recent research has shown that the mechanism of gain increasing, or outward adaptation, and the mechanism of gain decreasing, or inward adaptation, rely on partly different processes. We investigate how outward and inward adaptation of reactive saccades transfer to other types of saccades, namely scanning, overlap, memory-guided, and gap saccades. Previous research has shown that inward adaptation of reactive saccades transfers only partially to these other saccade types, suggesting differences in the control mechanisms between these saccade categories. We show that outward adaptation transfers stronger to scanning and overlap saccades than inward adaptation, and that the strength of transfer depends on the duration for which the saccade target is visible before saccade onset. Furthermore, we show that this transfer is mainly driven by an increase in saccade duration which is apparent for all saccade categories. Inward adaptation, in contrast, is accompanied by a decrease in duration and in peak velocity, but only the peak velocity decrease transfers from reactive saccades to other saccade categories, i.e. saccadic duration remains constant or even increases for test saccades of the other categories. Our results therefore show that duration and peak velocity are independent parameters of saccadic adaptation and that they are differently involved in the transfer of adaptation between saccade categories. Furthermore, our results add evidence that inward and outward adaptation are different processes.

Keywords

Saccade, adaptation, saccade dynamics, eye movements, learning
Introduction

Saccades are ballistic movements that bring visual objects to the part of the retina with highest acuity. Saccade accuracy is constantly monitored by the oculomotor system and requires the conjoined action of sensory stages and motor stages in the central nervous system. The oculomotor system compensates for saccadic inaccuracies by saccadic adaptation (Kommerell et al., 1976; Abel et al., 1978; Optican and Robinson, 1980). Saccadic inaccuracies can be artificially generated in the laboratory by a systematic intrasaccadic displacement of the saccade target (McLaughlin, 1967). This displacement generates a difference between the eye landing position and the post-saccadic visual location of the target. The error is compensated by manipulating the amplitude of saccades in subsequent trials. The location, timing, and consistency of the postsaccadic error are important factors for the effectiveness of saccadic adaptation (Wallman and Fuchs, 1998; Shafer et al., 2000; Noto and Robinson, 2001; Collins et al., 2009; Havermann and Lappe, 2010; Panouilleres et al., 2011).

Saccadic adaptation is specific to the direction (Deubel et al., 1986; Deubel, 1987), amplitude (Albano and King, 1989; Frens and Van Opstal, 1994) and starting position (Havermann et al., 2010) of the adapted saccade for which feedback is provided. However, if the same gain decrease feedback signal is provided for different saccade amplitudes and directions, adaptation affects all saccades at the same time (Garaas et al., 2008; Garaas and Pomplun, 2011; Rolfs et al., 2010). The amount by which adaptation transfers onto other saccades depends on the difference of these saccades to the adapted saccade (Albano, 1996; Frens and Van Opstal, 1994). Metric differences between the adapted saccade and the test saccade lead to the adaptation field, i.e. the transfer of adaptation to other amplitudes and directions (Frens and Van Opstal, 1994; Noto et al., 1999; Collins et al., 2007; Schnier et al., 2010). Differences in the starting position between adapted saccade and test saccade of the same amplitude and direction show a modulation of saccadic adaptation by eye position signals (Havermann et al., 2010). Non-metric transfer, i.e. transfer when the metrics of adapted and test saccade are the same, occurs between saccades of different category. Saccades can be categorized according to the stimuli or processes by which they are elicited. Reactive saccades are elicited by a sudden jump of a fixed target from the foveal to a peripheral location. Scanning saccades occur when one voluntarily shifts gaze from one object in a scene to another. In memory-guided saccades gaze is shifted to the remembered position of a target that is no longer visible. The main difference between reactive, scanning, and memory-guided saccades is the visual availability of the target and the fixation point. Whereas in scanning saccades both target and fixation point are constantly present, in memory-guided saccades the target is not visually
available and in reactive saccades the fixation point disappears when the target jumps to the periphery. Overlap and gap saccades introduce further variation of this parameter. In overlap saccades the target is presented together with the fixation point, but the saccade is initiated only when the fixation point is turned off. For gap saccades the fixation point is turned off even slightly before a saccade target appears (cf. Hopp and Fuchs (2004) for review).

Many studies have measured adaptation transfer between particular saccade types (Erkelens and Hullemann, 1993; Deubel, 1995, 1999; Fujita et al., 2002; Gaveau et al., 2005; Collins and Dore-Mazars, 2006; Cotti et al., 2007; Alahyane et al., 2008a, Hopp and Fuchs, 2010). They found that transfer is different between saccade types and often not symmetric. For example, scanning saccade adaptation transfers strongly to reactive saccades but the transfer from reactive to scanning saccades is weak (Alahyane et al., 2007; Collins and Dore-Mazars, 2006; Cotti et al., 2007; Deubel, 1999). There is little transfer from reactive saccades to overlap saccades but strong transfer in the opposite direction (Deubel, 1999). On the other hand there is an almost complete reciprocal adaptation transfer between reactive and gap saccades but only little reciprocal adaptation transfer between reactive and memory-guided saccades (Deubel, 1999). The differences in transfer suggest that adaptation of different saccade types occurs at different sites in the oculomotor system. Alahyane et al. (2007) argued for a combination of a single neuronal adaptation locus in the final common saccadic pathway and two partially overlapping loci specific to adaptation of reactive and voluntary saccades.

All of the above mentioned transfer studies were done with inward adaptation, i.e. the shortening of saccade amplitude. Outward adaptation, i.e. the lengthening of saccade amplitude, is known to use partially different mechanisms than inward adaptation (cf. Pelisson et al. (2010) for review). For example, outward adaptation takes longer to develop and is less efficient than inward adaptation (Miller et al., 1981; Fuchs et al., 1996; Ethier et al., 2008; Panouilleres et al., 2009; Straube et al., 1997; Scudder et al., 1998; Robinson et al., 2003). Moreover, outward adaptation is less stable than inward adaptation as shown by faster deadaptation of the outward adapted state (Straube et al., 1997). Furthermore, inward adaptation leads to a decrease in saccadic peak velocity (Fitzgibbon et al., 1985; Abrams et al., 1992; Straube et al., 1995, 1997) whereas outward adaptation shows no increase in peak velocity (Chen-Harris et al., 2008; Ethier et al., 2008). Ethier et al. (2008) suggested that an internal feedback signal is adjusted mid-flight during saccadic inward adaptation while the brain really learns to produce larger saccade amplitudes by target remapping during outward adaptation. Patients with lesions in the cerebellar vermis partially adapt in inward direction but completely lacked adaptation in outward direction (Golla et al., 2008). Because inward adaptation was very similar to a resilience experiment, which measures saccadic performance throughout many trials of the same amplitude, Golla et al. (2008) suggested that saccadic inward adaptation relies on substantial passive components as for example fatigue, and that saccadic outward adapta-
tion is an active process that requires selective increases in saccade duration. Differences between inward and outward adaptation were also shown in the firing patterns of the population burst of Purkinje cells in the cerebellum (Catz et al., 2008). Finally, recent behavioral studies revealed differences in adaptation transfer to anti-saccades (Panouilleres et al., 2009), to perceptual localization (Zimmermann and Lappe, 2010; Schnier et al., 2010), and to hand pointing (Hernandez et al., 2008). Differences were also found in the metric transfer pattern, suggesting a different pattern of spatial generalization between inward and outward adaptation fields (Frens and Van Opstal, 1994; Collins et al., 2007; Schnier et al., 2010; Semmlow et al., 1989).

In the present study we measured transfer between saccade types for outward adaptation, and compared transfer characteristics between inward and outward adaptation. In a first experiment we investigated adaptation transfer from reactive saccades to gap saccades, overlap saccades, memory-guided saccades, and scanning saccades. Differences between inward and outward adaptation in the amount of transfer occurred for the scanning and the overlap condition, i.e. for the voluntary saccade category. In both cases the transfer rate was higher for outward than for inward adaptation. Scanning and overlap saccades differ from reactive saccades in that the saccade target is visible for some time before saccade initiation. Thus the amount by which gain transfer differed between inward and outward adaptation for scanning and overlap saccades might be related to the presentation duration of the saccade target. Therefore, in a second experiment we investigated the influence of the duration of target presentation in the overlap condition on the adaptation transfer. We found that adaptation transfer from reactive saccades to overlap saccades with a long period of overlap was higher after saccadic outward adaptation than after saccadic inward adaptation. Finally, we analyzed saccadic duration and saccadic peak velocity to investigate the influences of the dynamic changes of the adapted reactive saccade on the dynamic of the tested saccade types. This also revealed differences between inward and outward adaptation.

**Methods**

**Experimental settings**

Stimuli were presented on a 21” monitor (Eizo FlexScan F930) with a vertical frequency of 120 Hz at a resolution of 1024 x 768 pixels. Participants were seated 57 cm in front of the stimulus monitor with their chin fixated in a supporting chin rest. This setting results in a visual field of 40 deg x 30 deg. Experiments were done in complete darkness with a background luminance below 0.0006 cd/m². The
low luminance was a result of our intention to remove all visible background stimulation and particularly the borders of the monitor screen, and to prevent effects of phosphor persistence of the monitor. Because of this the monitor was covered with a dark foil that reduced the luminance by about two log units, i.e. background luminance was not visible anymore and all stimuli were reduced in luminance (see Georg et al. (2008) for a detailed description).

**Eye movement recording**

Eye movements were recorded with an EyeLink 1000 eye tracker (Desktop Mount Base System, SR Research, LTD, Canada). Subjects had to perform all experimental sessions binocular with only the left eye tracked. All data, including online events, raw gaze position samples (at 1000 Hz), and messages corresponding to the course of the program were recorded. During experimental sessions the eye tracker detected the pupil as well as the corneal reflex. These measurements were checked against each other to compute the final gaze position. Data were offline checked for drifts that might have occurred. No drifts were detected. Saccades were detected online as soon as eye velocity crossed a velocity threshold of 22 deg/sec and an acceleration threshold of 4000 deg/sec².

**Procedure for reactive saccade adaptation**

Fixation point (FP) and target (T1) were red disks with a radius of 0.5 deg and a luminance of 0.13 cd/m². Both disks were clearly visible under photopic conditions (cf. Georg et al. (2008)). At the beginning of each trial FP was presented 12 deg to the left of the center of the screen. Correct fixation was checked online. After a variable time between 500 and 1100 ms the fixation point disappeared and subjects had to perform a saccade towards the simultaneously appearing target T1, which was 8 deg to the right of the center of the screen. Saccade onset was detected online when the eye position was exceeding a three deg trigger threshold rightwards from fixation point. At this time the saccade target T1 stepped 6 deg inwards, or 6 deg outwards, to location T2. The direction of the step (inward/outward) depended on the particular experimental session and never changed within a session. T2 remained visible for further 300 ms after saccade onset. 550 ms later the next trial began.

**Procedures for test saccades**

**Reactive test saccades**
Reactive test saccades were elicited with the same procedure that was used for reactive saccade adaptation except that the saccade target T1 was extinguished after saccade onset when eye position exceeded a three deg threshold rightwards from the fixation point.

**Gap test saccades**

300 ms after the subject has established fixation the radius of FP was slowly decreasing until FP completely vanished. This procedure took further 800 ms and should prevent subjects from falsely reacting on the extinction of the fixation point. Preliminary experiments had shown that because the different task types were intermixed in each session, many subjects had difficulties in keeping fixation when the fixation point was turned off. In the reactive, overlap, and memory-guided tasks the extinction of the fixation point coincided with the go-signal of the saccade. We designed the gradual fading of the fixation point in our gap condition to help the subjects keep fixation and shield them from any unwanted reaction triggered by sudden fixation point offset. At a variable time between 400 and 1000 ms after the fixation point had completely disappeared the target T1 appeared and subjects had to perform the saccade towards the target. The target was extinguished after saccade onset.

It is important to realize that our particular gap saccade condition differed from standard gap saccade conditions in several aspects. First, there is the slowly and gradual disappearance of the fixation point. Second, there is the large and variable gap duration of between 400 and 1000 ms, which was chosen to make our gap condition comparable to the overlap saccade condition. Most other studies used gaps of about 200 ms (Fuchs et al. 1996; Deubel, 1999; Hopp and Fuchs, 2010). Because of the difference in fixation point offset and gap duration our gap condition cannot and should not be equated to a regular gap saccade condition. For example, our gap condition did not evoke express saccades. However, we will use the term gap saccades in the course of this study for all saccades performed in our particular setup.

**Memory-guided test saccades**

In memory-guided trials FP appeared for a variable time between 500 and 1100 and correct fixation was checked. Then T1 was presented for 200 ms while subjects continuously fixated FP. After a variable time between 400 and 1000 ms FP disappeared and subjects had to perform a saccade towards the remembered position of T1. 1050 ms after the saccade the next trial began.

**Overlap test saccades**

In overlap trials FP appeared for a variable time between 500 and 1100 and correct fixation was checked. Then T1 appeared together with FP for a variable time between 400 and 1000 ms indicating the overlap
duration. Thereafter FP disappeared and subjects had to perform a saccade towards T1. After saccade onset, i.e. when eye position exceeded a three deg threshold rightwards from the fixation point, T1 was extinguished.

In the second experiment of this study overlap test saccades were measured with seven different overlap durations, i.e. 0 ms, 150 ms, 250 ms, 400 ms, 700 ms, 1400 ms, and 2500 ms.

**Scanning test saccades**

At the beginning of a scanning trial, FP and T1 were presented together with two further targets (A and B) of identical size, shape, and luminance. A and B were located 12 deg above T1 and FP, respectively. Therefore, the four targets formed a rectangle of width 20 deg and height 12 deg. Subjects were instructed to first look at A, then move their eyes to B, then to FP, and finally to T1. They were instructed to do this voluntarily and at their own pace, as they would scan an image. During each of these saccades the previously fixated target disappeared, i.e. A disappeared when eye position exceeded a three deg threshold leftwards from A and B disappeared when eye position exceeded a three deg threshold downwards from B. During the last saccade, the saccade from FP to T1, T1 also disappeared when eye position exceeded a three deg threshold rightwards from the fixation point FP.

**Course of the experiments**

An experimental session of the first experiment consisted of 250 pre-adaptation trials, 300 adaptation trials, and 250 post-adaptation trials. Pre-adaptation phase and post-adaptation phase were divided into 5 blocks of 50 trials, each testing one particular saccade type (gap, memory-guided, scanning, overlap, or reactive). Each block started with 5 test saccades followed by 10 reinforcing reactive saccades. Then again 5 test saccades were performed followed again by 10 reactive saccades. Finally, 5 test saccades were performed followed by 15 reactive saccades (see Figure 1). Reinforcing reactive saccades were without the target step from T1 to T2 in the pre-adaptation phase, but with this target step in the post-adaptation phase. The five blocks were presented in random order, each with one type of test saccade. The order of blocks was identical in pre- and post-adaptation phases of a single session. A computer voice announced each particular block of test saccades.

In the adaptation-phase, 75% of trials were reactive adaptation trials with the corresponding inward or outward target step. The remaining 25% of trials induced reactive saccades to randomly chosen targets 12 deg directly above or below FP. In these trials the target was extinguished during the saccade and thus
did not induce adaptation. These trials served to prevent stereotypic behavior during the adaptation phase. Each subject participated in two sessions in random order, one with saccadic inward adaptation and the other with saccadic outward adaptation.

Experimental sessions of the second experiment consisted of 210 pre-adaptation trials, 300 adaptation trials, and 210 post-adaptation trials. Adaptation trials were identical to those of the first experiment. The pre- and post-adaptation phases contained blocks of overlap test saccades with different durations of overlap. In each block, 5 test saccades were followed by 10 reactive reinforcing saccades, followed by the same 5 test saccades, and finally, 10 reactive reinforcing saccades. Thus there were 30 trials in each block. Seven different test overlap durations (0 ms, 150 ms, 250 ms, 400 ms, 700 ms, 1400 ms, or 2500 ms) were tested in different blocks, each with one type of test overlap duration. Blocks were presented in random order but with the same order in pre- and post-adaptation phases in each session. Each subject completed four sessions in random order, two experimental sessions with inward adaptation and two with outward adaptation.

Participants

Eight subjects (2 females, 6 males, 1 author, 7 naive, age range: 21-38 years) participated in all experimental sessions of the first experiment, nineteen subjects (12 females, 7 males, 1 author, 18 naive, age range: 20-38 years) in all experimental sessions of the second. Six subjects of the first experiment also participated in the second experiment (2 females, 4 males, 1 author, 5 naive, age range: 21-38). Two subjects (2 females, 22 and 25 years) in the second experiment were excluded from the data analysis because they exhibited too little adaptation to allow a meaningful transfer analysis. Thus, data analysis in the second experiment was done with 17 subjects. All subjects had normal or corrected to normal vision, and had participated in other eye movement sessions before the experiment. Before starting the experiment participants gave informed consent in accordance with the Declaration of Helsinki.

Data analysis

Mathematica 7.0 was used for all data analysis. Except for the scanning condition first saccade in each trial was used for data analysis. In the scanning saccade test condition the first saccade after the eye had landed on FP was used for data analysis. For a saccade to enter analysis, its start point had to be within a circle of 2.5 deg diameter around the fixation point, its amplitude had to be between 10 and 30 deg, its duration had to be between 20 and 100 ms, and its latency had to be between 80 and 400 ms. The
latency criterion was used for all but the scanning trials, for which latency had to be between 80 ms and 1000 ms. In the first experiment 91.9 % ± 6.5 (SD) of all saccades in the inward adaptation sessions and 96.5 % ± 3.4 (SD) of all saccades in the outward adaptation sessions were accepted for data analysis. In the second experiment 91.8 % ± 6.2 (SD) of all saccades in the inward adaptation and 93.6 % ± 6.7 (SD) of all saccades in the outward adaptation sessions were accepted.

Adaptation transfer from reactive saccades to each of the test conditions was computed by taking the median saccade amplitudes in pre- and post-adaptation phase and calculating the gain change in each saccade condition according to

\[
\text{gain change}\% = \left( \frac{\text{amplitude}_{\text{post}} - \text{amplitude}_{\text{pre}}}{\text{amplitude}_{\text{pre}}} \right) \times 100.
\]

This gain change was compared with the gain change of the reactive saccades. Latencies were computed by taking the time of saccade start from T1 onset for reactive and gap saccades, FP offset for overlap and memory-guided saccades, and fixation onset at FP for scanning saccades. Saccade velocities were computed by taking the mean of seven neighbouring samples in a saccade. The maximum of each velocity curve determined the saccadic peak velocity.

### Results

#### Adaptation transfer from reactive saccades to other saccade categories

Figure 2 about here

Figure 2 shows example sessions for inward and outward adaptation. The black crosses give the amplitudes of reactive saccades in the pre-adaptation, adaptation, and post-adaptation phases. Clearly, there is a reduction in saccade amplitude for inward adaptation and an increase in amplitude for outward adaptation (cf. gray rectangles). The symbols show the amplitudes of test saccades of the gap (empty circles), memory-guided (empty triangles), overlap (filled circles), and scanning (filled triangles) saccades. Plus signs show the amplitudes of reactive test saccades, which differed from reactive adaptation saccades in that the target was extinguished during the saccade. Clearly, the amount of adaptation shown in the post-adaptation test phase differed between saccade categories.
Adaptation

Averaged over all subjects, the mean amplitude of reactive saccades in the pre-adaptation phase was 18.91 deg ± 0.24 (SE), indicating a slight hypometria. The adaptation gain change, i.e. the mean amplitude change was -24.7 % ± 2.0 (SE) after inward adaptation and 19.7 % ± 1.6 (SE) after outward adaptation (expected maximum gain change for 20 deg saccades with a ± 6 deg step size is ± 30 %). The gain change was significantly lower in the outward compared to the inward adaptation (paired t-test with absolute values, p<0.0005). During inward adaptation mean latency increased from 195.7 ms ± 2.6 (SE) to 217.3 ms ± 4.8 (SE) (paired t-test, p<0.0005), mean duration decreased from 66.1 ms ± 1.2 (SE) to 60.7 ms ± 1.6 (SE) (paired t-test, p<0.005), and mean peak velocity decreased from 473 deg/s ± 16 (SE) to 397 deg/s ± 14 (SE) (paired t-test, p<0.0005).

During outward adaptation mean latency increased from 196.0 ms ± 1.9 (SE) to 205.3 ms ± 3.0 (SE) (paired t-test, p<0.05) and mean duration increased from 65.8 ms ± 1.4 (SE) to 73.4 ms ± 0.9 (SE) (paired t-test, p<0.0005). Mean peak velocity remained almost constant (Pre: 476 deg/s ± 9 (SE), Post: 485 deg/s ± 11 (SE) (paired t-test, p=0.14).

Transfer

Figure 3 shows the mean amplitudes of all test saccade types in the pre- and post-adaptation phases. In the pre-adaptation phase, overlap, scanning, and memory-guided test saccades were more accurate than gap and reactive test saccades. The errors of gap and reactive test saccades were about 1 deg, those of overlap, scanning, and memory-guided test saccades about 0.3 deg or less (see also Table 1 for a detailed analysis).

After inward adaptation a one-way repeated measures ANOVA on the amplitudes revealed a significant difference between saccade types (F(4,28)=17.92, p<0.0005). Post-hoc t-tests showed that the mean amplitude of reactive test saccades was significantly smaller than the mean amplitudes of overlap saccades (p<0.005), scanning saccades (p<0.0005), and memory-guided saccades (p<0.005). The amplitude difference to gap saccades was only marginally significant (p=0.06). The mean amplitude of gap saccades was significantly smaller than the mean amplitude of overlap saccades (p<0.005), memory-guided saccades (p<0.05), and scanning saccades (p<0.0005). The mean amplitude of overlap saccades was significantly smaller than the mean amplitude of scanning saccades (p<0.05).

Also after outward adaptation a one-way repeated measures ANOVA showed a significant difference be-
tween saccade types (F(4,28)=3.32, p<0.05). Post-hoc t-test analysis revealed significant differences between reactive test saccades and gap saccades (p<0.005) and marginally significant differences between reactive test saccades and scanning saccades (p=0.08). The mean amplitudes of reactive, overlap, and memory-guided saccades were very similar to each other (p>0.25 in any comparison).

Figure 4 shows the percent gain transfer (PGT), which is defined as

\[ \text{PGT} = \frac{\text{gain change}\% \text{ (tested)}}{\text{gain change}\% \text{ (adapted)}} \times 100. \]

A two-way repeated measures ANOVA with the factors saccade types (reactive, gap, overlap, scanning, memory-guided) and adaptation direction (inward/outward) revealed main effects of saccade type (reactive, gap, overlap, scanning, memory-guided, F(4,28)=36.93, p<0.0005) and adaptation direction (inward/outward, F(1,7)=8.56, p<0.05) and a significant interaction (F(4,28)=2.88, p<0.05). Post-hoc t-test analysis showed that for inward adaptation (Figure 4A) the PGT of reactive test saccades (87.2 % ± 5.1 (SE)) was significantly higher than the PGTs of overlap saccades (39.4 % ± 7.2 (SE)) (p<0.005), scanning saccades (18.0 % ± 4.5 (SE)) (p<0.0005), and memory-guided saccades (40.3 % ± 8.9 (SE)) (p<0.005), and with a tendency to be higher than the PGT of gap saccades (61.3 % ± 8.5 (SE)) (p=0.06). The PGT of scanning saccades was significantly smaller than the PGTs of all other saccade types (reactive, gap (p<0.0005), overlap (p<0.005), memory-guided (p<0.05)). The PGT of gap saccades was significantly higher than the PGT of overlap saccades (p<0.05). No significant PGT difference was observed between memory-guided saccades and overlap saccades (p=0.93).

For outward adaptation (Figure 4B) the PGT of reactive test saccades (90.5 % ± 4.3 (SE)) was significantly higher than the PGTs of gap saccades (61.6 % ± 5.0 (SE)) (p<0.005), scanning saccades (43.7 % ± 6.0 (SE)) (p<0.0005), and memory-guided saccades (43.4 % ± 7.1 (SE)) (p<0.0005), and with a tendency to be higher than the PGT of overlap saccades (75.1 % ± 4.8 (SE)) (p=0.07). The PGT of overlap saccades was significantly higher than the PGT of scanning saccades (p<0.05) and memory-guided saccades (p<0.05). The PGT of gap saccades was significantly higher than the PGT of scanning and memory-guided saccades (p<0.05).

It is interesting to note that for both adaptation directions the reactive test saccades showed only about 90 % of the adaptation of the reactive saccade during the adaptation. This significantly diminished gain transfer (t-test, p<0.05) was not due to deadaptation within the block of 5 test saccades. Instead, subjects might have been biased to perform test saccades somewhat differently from the standard reactive saccades because each block of test saccades was announced by a computer voice.
Differences in transfer between inward and outward adaptation

The intention of our study was to look for differences in the transfer between inward and outward adaptation. Therefore, we compared the adaptation transfer rates between inward and outward adaptation for each saccade category with post-hoc t-tests. Differences in gain transfer between inward and outward adaptation occurred for overlap and scanning saccades. In both cases, the PGT was higher after outward adaptation than after inward adaptation (overlap: p<0.05; scanning: p<0.005). No PGT differences were found for gap and memory-guided saccades (gap: p=0.97, memory-guided: p=0.82). Thus, PGT differences between inward and outward adaptation occurred only for those saccade types, for which the presentation duration of the saccade target was prolonged in comparison to the reactive saccade.

Figure 5 about here

Transfer effects on other saccade parameters

Since outward adaptation and inward adaptation affect saccadic peak velocity and duration differently, we analyzed durations and peak velocities in all tested saccade types to investigate how parameter changes of the adapted reactive saccade transferred to the test saccades. Figure 5 shows the mean saccade durations and peak velocities of each saccade type before and after adaptation (see also Table 1 for a detailed analysis). Before adaptation, durations and peak velocities differed between saccade types (one-way repeated measures ANOVA, duration: F(4,28)=19.75, p<0.0005; peak velocity: F(4,28)=33.73, p<0.0005). Post-hoc t-tests revealed that memory-guided saccades and overlap saccades had significantly longer durations than the other test saccades (p(max)<0.05). These differences were considerably more pronounced for the memory-guided saccades (p<0.005 in any case). Memory-guided saccades also had significantly smaller peak velocities than the other saccade types (p(max)<0.005). This also applied to overlap saccades in comparison to most other saccade types (p(max)<0.05) except for the gap saccade type (p=0.24).

After inward adaptation, mean duration and peak velocity of the reactive test saccades decreased (paired t-tests, p<0.005 (duration), p<0.0005 (peak velocity)). Mean peak velocity also decreased in the other saccade types (paired t-test, p(max)<0.05), but mean duration of these test types slightly increased. Thus, in the post-adaptation phase the mean duration of reactive test saccades was significantly lower than the mean duration of any other saccade type (one-way repeated measures ANOVA, F(4,28)=22.09, p<0.0005, post-hoc t-tests: p(max)<0.005). This is an unexpected finding which suggests that the adaptation of
reactive saccades is due to a decrease in velocity and in duration, whereas the transfer to other saccade
categories is only carried by the peak velocity decrease.

After outward adaptation, mean duration increased significantly in all test saccade types (paired t-tests,
p(max)<0.005) while mean peak velocity remained constant.

Table 1 about here

**Duration of target presentation in the overlap condition**

The above experiment revealed a stronger adaptation transfer for outward than for inward adaptation for
overlap and scanning saccades. Scanning saccades differ from reactive saccades in that they are internal-
ly (voluntarily) triggered rather than reacting to an external event such as target appearance. Thus, one
might suggest that outward adaptation affects the pathway for voluntary saccade generation more than
inward adaptation. Overlap saccades, on the other hand, are similar to reactive saccades in that they are
triggered by the offset of the fixation point. They are, however, similar to scanning saccades in that the
target is visible for an extended time before the beginning of the saccade. In this view, differences be-
tween reactive saccades on the one hand and overlap and scanning saccades on the other hand may arise
from the availability of the saccade target before saccade programming. Indeed, the transfer of inward
adaptation from reactive saccades to overlap saccades shows a continuous, monotonic dependence on
overlap duration (Deubel, 1999). Transfer is strong for short overlap durations and decreases with in-
creasing duration. This suggests that some pathways of saccade generation integrate target information
over an extended period of time, and that these pathways are not adapted in the reactive saccade condi-
tion. To test, whether these pathways are differently involved in outward than in inward adaptation we
decided to measure transfer of outward adaptation from reactive saccades to overlap saccades with vary-
ing durations of overlap, and compare it to transfer of inward adaptation.

Adaptation of reactive saccades was induced in the same manner as in the first experiment. In the pre-
and post-adaptation phases, overlap saccades with seven different overlap durations were tested: 0 ms,
150 ms, 250 ms, 400 ms, 700 ms, 1400 ms, or 2500 ms. These overlap saccades were tested in blocks of
5, interspersed with 10 reinforcing reactive saccades. Note that the 0 ms overlap condition is the identical
to the reactive saccade condition, only that it was announced by the computer voice as an overlap block.
Saccade parameters in the pre-adaptation phase

Because our paradigm combined trials of overlap saccades with different overlap duration we analyzed saccade amplitudes in the pre-adaptation phase for the different overlap durations. Saccadic accuracy increased with increasing overlap between 0 and 400 ms. At 0 ms overlap mean saccade amplitude was 19.75 deg ± 0.19 (SE), or 0.25 deg below the target amplitude of 20 deg. At 400 ms overlap mean saccade amplitude was 19.96 deg ± 0.19 (SE) or 0.04 deg below target amplitude. For even longer overlap duration accuracy dropped again. At 2500 ms overlap mean saccade amplitude was 19.62 deg ± 0.24 (SE), or 0.38 deg below target amplitude. Although these variations were rather small, they were supported by a one-way repeated measures ANOVA (F(6,96)=2.50, p<0.05).

The duration of target presentation also influenced saccade dynamics. Saccade duration increased with increasing overlap duration from 67.5 ms ± 0.9 (SE) at 0 ms overlap to 72.2 ms ± 2.2 (SE) at 2500 ms overlap. Peak velocity decreased with increasing overlap from 504 deg/s ± 10 (SE) at 0 ms overlap to 460 deg/s ± 10 (SE) at 2500 ms overlap. The increase of duration and decrease of peak velocity was especially strong in the shorter overlap periods between 0 ms and 400 ms.

Adaptation

Figure 6 shows example sessions for inward and outward adaptation. Clearly amplitudes decreased during the inward adaptation procedure and increased during the outward adaptation procedure. Furthermore, the amount of transfer shown in both post-adaptation test phases (Figures 6A and 6B) differed between different overlap test conditions.

Averaged over all subjects, the mean saccadic amplitude decreased during inward adaptation from 19.40 deg ± 0.17 (SE) to 14.55 deg ± 0.28 (SE), which corresponds to a gain decrease of -25.1 % ± 1.0 (SE) (expected maximum gain change for 20 deg saccades with a -6 deg step size is -30 %). During outward adaptation, the mean saccadic amplitude increased from 19.34 deg ± 0.15 (SE) to 22.94 deg ± 0.22 (SE), which corresponds to a gain increase of 18.6 % ± 0.9 (SE) (expected maximum gain change for 20 deg saccades with a 6 deg step size is 30 %). The gain change after saccadic outward adaptation was significantly lower than the gain change after saccadic inward adaptation (paired t-test with absolute values, p<0.0005).

During inward adaptation mean latency increased from 200.2 ms ± 3.9 (SE) to 210.8 ms ± 3.8 (SE) (paired t-test, p<0.0005), mean duration decreased from 66.2 ms ± 0.8 (SE) to 59.2 ms ± 0.8 (SE) (paired t-
t-test, \(p<0.0005\), and mean peak velocity decreased from 499 deg/s ± 10 (SE) to 432 deg/s ± 14 (SE) (paired t-test, \(p<0.0005\)).

During outward adaptation mean latency increased from 201.8 ms ± 2.9 (SE) to 209.9 ms ± 2.8 (paired t-test, \(p<0.0005\)), mean duration increased from 66.7 ms ± 1.1 (SE) to 77.3 ms ± 1.8 (SE) (paired t-test, \(p<0.0005\)), and mean peak velocity remained constant (Pre: 503 deg/s ± 10 (SE), Post: 500 deg/s ± 12 (SE) (paired t-test, \(p=0.30\)).

Transfer

After inward adaptation, saccade amplitudes were reduced in all overlap conditions, but amplitude reduction decreased with longer overlap duration. Similarly, outward adaptation led to larger amplitudes in all overlap conditions, but amplitudes became smaller for longer overlap. Thus, the transfer from reactive saccades to overlap saccades depended on the duration of the overlap.

Figure 7 about here

Figure 7 shows the percent gain transfer PGT for each overlap test condition. PGT was high for short overlap durations. As in the first experiment of this study the percent gain transfer to overlap test saccades with 0 ms period of overlap, i.e. reactive test saccades, was not 100 % but only about 85 % and thus significantly diminished (t-test, \(p<0.05\), see first experiment for explanation). PGT decreased exponentially for longer overlap durations. This was true for both adaptation directions. However, the final level of gain transfer was higher for outward than for inward adaptation. While inward adaptation of reactive saccades transfered to 43 % ± 5 (SE) to overlap saccades with 2500 ms period of overlap, outward adaptation transfered to 63 % ± 5 (SE). Our observations were supported by a two-way repeated measures ANOVA with the factors overlap duration (0 ms, 150 ms, 250 ms, 250 ms, 400 ms, 700 ms, 1400 ms, 2500 ms) and adaptation direction (inward/outward). This ANOVA showed a significant dependence of the PGT on overlap durations (\(F(6,96)=14.65, p<0.0005\)) and a significant interaction between overlap duration and adaptation direction (\(F(6,96)=2.56, p<0.05\)), confirming that the decrease of the PGT with increasing overlap duration was stronger after inward adaptation than after outward adaptation.

We also investigated whether the PGT differences in this experiment might have been a function of latency rather than of overlap duration. This might have been the case because saccades with short overlap durations had shorter latencies than saccades with long overlap durations. Baseline latencies before adaptation increased with overlap duration from 214.9 ms ± 5.3 (SE) at 0 ms overlap to 242.5 ms ± 7.1 (SE)
at 2500 ms overlap (ANOVA, F(6,96)=4.88, p<0.0005). Moreover, latencies slightly increased after both inward and outward adaptation (mean increase after inward adaptation: 10.5 ms ± 2.7 (SE), p<0.005;
mean increase after outward adaptation: 8.2 ms ± 2.1 (SE) p<0.005), but without a systematic dependence on overlap duration.

Thus, we tested for a covariation between saccade latency and gain transfer within each overlap duration by linear regressions of latencies versus saccade amplitudes before adaptation and linear regressions of latencies versus saccade amplitudes after adaptation for each of the tested overlap durations. Regression slopes were all flat, i.e. they never exceeded a value of ± 0.008 deg/ms. The same applied to linear regressions of binned latencies versus binned difference between post-adaptation amplitudes and pre-adaptation amplitudes. Thus, this analysis showed no indication that latency within an overlap duration affected the amount of transfer.

**Transfer effects on other saccade parameters**

We also looked for transfer effects of saccadic duration and peak velocity in the different overlap conditions. After inward adaptation, mean duration at 0 ms overlap period decreased by 6.6 ms ± 0.9 (SE) (t-test against zero, p<0.0005), which was consistent with the mean duration decrease of the reactive saccades. For longer periods of overlap this duration decrease diminished down to a value of 0.5 ms ± 0.8 (SE) at 2500 ms overlap period. A one-way repeated measures ANOVA showed a significant dependence of the duration decreases on the overlap duration (F(6,96)=12.31, p<0.0005) (cf. Figure 8). Inward adaptation diminished peak velocities in the same manner as the mean peak velocity of the adapted saccade itself, on average by about 60 deg/s, independent of the overlap duration (ANOVA, F(6,96)=1.11, p=0.36).

Outward adaptation increased mean duration by about 10 ms for all overlap durations. No significant differences were found between overlap durations (ANOVA, F(6,96)=0.56, p=0.75). Also for peak velocity changes there was no significant dependence on overlap duration, i.e. mean peak velocity changes after outward adaptation were slightly beyond zero for all overlap durations (ANOVA, F(6,96)=1.71, p=0.13).

Thus, in accordance with the first experiment, the transfer of saccadic inward adaptation was largely based on a peak velocity decrease whereas the transfer of saccadic outward adaptation was based on a duration increase.

Figure 8 about here
Discussion

Adaptation transfer

We measured the transfer of inward and outward saccadic adaptation from reactive to gap, overlap, scanning, and memory-guided saccades. These experiments were prompted by recent observations that inward and outward saccadic adaptation rely on partially different neuronal mechanisms. We found that transfer to gap and memory-guided saccades was similar for inward and outward adaptation, but transfer for overlap and scanning saccades was stronger for outward than for inward adaptation. Furthermore, we found that the strength of transfer to overlap saccades depended on the duration of the overlap. In the following, we will first discuss differences between inward and outward adaptation and between different saccade categories, then we will discuss possible mechanisms for the two adaptation types.

Saccadic outward adaptation takes longer to develop, reaches lower gain change levels and is less stable than saccadic inward adaptation (Miller et al., 1981; Straube and Deubel, 1995; Fuchs et al., 1996; Straube et al., 1997; Scudder et al., 1998; Robinson et al., 2003; Ethier et al., 2008; Panouilleres et al., 2009). Outward and inward adaptation affect saccade dynamics differently. Saccades after saccadic outward adaptation have similar dynamics as non-adaptated saccades of the same amplitude, whereas saccades after inward adaptation show decreased peak velocity (Fitzgibbon et al., 1985; Abrams et al., 1992; Straube et al., 1995, 1997; Chen-Harris et al., 2008; Ethier et al., 2008).

Outward adaptation shows a stronger transfer to perception (Zimmermann and Lappe, 2010; Schnier et al., 2010) and hand pointing (Hernandez et al., 2008) than inward adaptation and a different pattern of transfer to other saccade amplitudes (Semmlow et al., 1989; Collins et al., 2007; Schnier et al., 2010). Furthermore, it was shown that outward adaptation shows less transfer to anti-saccades in the adapted direction than inward adaptation (Panouilleres et al., 2009). Our results add a different pattern of transfer to other saccade categories.

Transfer between saccade categories has, up to now, been studied only for saccadic inward adaptation. Adaptation transferred strongly from reactive to gap saccades and much weaker to overlap, scanning, or memory-guided saccades (Erkelens and Hulleman, 1993; Deubel, 1999; Fujita et al., 2002; Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2009; Zimmermann and Lappe, 2009, Hopp and Fuchs, 2010). Our results for inward adaptation are consistent with those findings.

The differences in transfer from reactive saccades to other saccade categories, along with observations of an often stronger transfer in the opposite direction (Alahyane et al., 2007; Collins and Dore-Mazars, 2006; Cotti et al., 2007), have led to the proposal of different loci of adaptation for different saccade cat-
categories, one for reactive and gap saccades, one for voluntary (delayed, overlap, scanning) saccades, and
one for memory-guided saccades (Deubel, 1999). However, a common locus must also exist because
otherwise there should be zero transfer between categories. In a two-level scheme proposed by Alahyane
et al. (2007), a single locus at a low level of the final common pathway contributes to adaptation of vol-
untary and reactive saccades, while partially overlapping loci at higher levels are specific to each sac-
cade type. These more specific loci might involve various areas of the oculomotor pathways, such as the
brainstem, cerebellum, or thalamo-cortical circuits, some of which are closer to the motor side of saccade
performance and some closer to visual target registration and movement planning (Hopp and Fuchs,
2002; Gaymard et al., 2001; MacAskill et al., 2002; Alahyane et al., 2008b; Pelisson et al., 2010).
Our data showed a significantly higher transfer from reactive to overlap and scanning saccades after
outward adaptation than after inward adaptation. No difference was found between the gap and memory-
guided conditions. This suggests that outward adaptation of reactive saccades modulates the pathway for
overlap and scanning saccades more than saccadic inward adaptation. Thus we must ask at which neu-
ronal stage outward adaptation of reactive saccades differs from inward adaptation of reactive saccades.
The first possibility is that both adaptation mechanisms differ at the motor stages. In this view, outward
adaptation of reactive saccades affects the motor stages of the pathway for overlap and scanning sac-
cades more than saccadic inward adaptation. This implies that differences between inward and outward
adaptation would occur rather late in oculomotor processing, at least after the sensory-motor transforma-
tions, and that perception should be unaffected after both adaptation methods. This, however, disagrees
with studies, which revealed adaptation transfer to perception (Zimmermann and Lappe, 2010; Schnier et
al., 2010) and hand-pointing (Hernandez et al., 2008) after outward adaptation and suggested that out-
ward adaptation, at least partially, relies on changes of the visual registration of the target. Thus, a
second possibility appears more likely, namely, that the outward adaptation mechanism differs from the
inward adaptation mechanism at the target registration or planning stages. In this view, there might be a
contribution of the target localization stages to outward adaptation even in the reactive saccade para-
digm. Whenever these stages are used after adaptation of reactive saccades, differences between saccadic
inward and outward adaptation should occur. Thus, we suggest that transfer differences between inward
and outward adaptation depend on the use of target localization stages that are more strongly modulated
after outward adaptation than after inward adaptation.
However, this suggestion does not imply that inward and outward adaptation are completely different at
all saccade relevant stages of the CNS. We have to consider at least both above mentioned stages of
adaptation, i.e. the motor stage and the target localization or planning stage. While we suggest differenc-
es between saccadic inward and outward adaptation at the planning stage, adaptation at the motor stage
might be rather similar for both adaptation directions. The involvement of such a common stage for in-
ward and outward adaptation might explain why the transfer from reactive to overlap saccades decreases with increasing overlap duration for both adaptation directions. Adaptation differences between inward and outward adaptation at the planning stage are then necessary to explain why the amount of transfer from reactive saccades to overlap and scanning saccades is higher after outward than after inward adaptation.

Overlap and scanning saccades differ from reactive, gap, and memory-guided saccades in that the target is visible for a long time before saccade initiation. Thus, the visual system has more time to register the target location, or to plan the saccade while the target is visible. Indeed, in the pre-adaptation phase of the overlap experiment saccades became more accurate as overlap duration increased from 0 ms to 400 ms, indicating that a longer target viewing leads to better saccade execution. On the other hand, reactive, gap, and memory-guided saccades are known to involve processes of motor preparation or anticipation if the upcoming target location is known (Paré and Munoz, 1996; Rolfs and Vitu, 2007; Dorris and Munoz, 1998). Overlap and scanning saccades may involve less of such motor preparation activity because the target is visible and can be used directly for the saccade planning. One might thus speculate that in overlap and scanning conditions the target representation or the saccade planning becomes more accurate because some neurons, or some stages along the oculomotor pathway, have long integration periods, and contribute weakly to saccades that are generated in immediate response to target appearance and are more influenced by anticipatory preparation signals. If these long integration neurons are less contributing to reactive saccade generation they may not be involved in reactive saccade adaptation. Their contribution to scanning and long-duration overlap saccades may then explain why these saccades do not show much transfer. Consistent with this, the transfer from reactive saccades to overlap saccades depended on the duration of the overlap. For inward adaptation, these results replicate Deubel (1999). For outward adaptation, our study shows that a similar dependency exists, and that the transfer at long overlap duration is larger than for inward adaptation.

Duration and peak velocity

We analyzed the mean duration and peak velocity of all tested saccade types. Inward adaptation of reactive saccades resulted in a duration decrease and a peak velocity decrease. Outward adaptation of reactive saccades, on the other hand, resulted in a duration increase only with no change in peak velocity. Because of the dynamic similarities between inward adaptation and resilience, a paradigm in which saccades of the same amplitude are performed for many trials, Golla et al. (2008) suggested that inward adaptation contains a substantial passive component of fatigue, whereas outward adaptation is an entirely active process that requires selective increases in saccadic duration. In comparing the dynamics of
adapted saccades with non-adapted saccades of the same amplitude, Ethier et al. (2008) showed that the velocity profile was very similar after outward adaptation but exhibited a drop in peak velocity after inward adaptation. They suggested that inward adaptation results from a change in internal feedback signal that has to be adjusted midflight, during the saccade. In contrast to this, during outward adaptation the brain learns to produce larger saccade amplitudes by target remapping.

In this view, dynamic differences between inward and outward adaptation may have different consequences on the dynamic of different test saccades. Thus, we investigated the change of peak velocity and mean duration of the tested saccade types in relation to the inward or outward adapted reactive saccade.

Figure 5 revealed that after saccadic inward adaptation the mean duration decreased, but only for the adapted reactive saccade. The other test saccades instead showed a slight duration increase. Peak velocity, on the other hand, decreased for all tested saccades. The decrease of peak velocity may be in part due to fatigue effects that occur for repetitive saccades of the same amplitude. Golla et al. (2008) found that peak velocity decreased during a resilience experiment in which 600 reactive saccades were made to the same target. Duration increased during this experiment so that saccade amplitude remained accurate. However Golla et al. (2008) also found that the peak velocity decrease can only account for parts of the inward adaptation mechanism because the dynamic changes during the resilience experiment were smaller and slower than during adaptation. Thus, considering these results and our findings we suggest that peak velocity decrease and duration decrease are two independent parameters in inward adaptation.

Velocity decrease transfers between saccade categories, but duration does not and instead even counteracts the transfer between saccade categories. The duration increase observed for gap, overlap, scanning, and memory-guided saccades increases their amplitudes and diminishes the adaptation effect. This is consistent with suggestions that the velocity decrease provides a general way to reduce saccade amplitude and that the duration is adjusted to fine-tune the saccade midflight to reach the target (Catz et al., 2008; Chen-Harris et al., 2008; Ethier et al., 2008; Golla et al., 2008).

After outward adaptation, mean duration increased for the reactive test saccades as well as for all other test saccades. Mean peak velocity remained largely constant in all conditions. Therefore, the transfer from reactive saccades to the other saccade categories must rely on the duration increase only. However, our observation that peak velocity remained constant might also show an influence of fatigue. Because saccade amplitudes increased during outward adaptation, peak velocity should have increased by about 30 deg/s if the saccades follow the main sequence (Lebedev et al., 1996).

The results of our first experiment were largely consistent with the results of our second experiment, in which inward adaptation of reactive saccades influenced mean duration of overlap saccades dependent on the overlap duration. Mean durations were less and less influenced as the overlap became longer. Peak velocity, on the other hand, did not depend on overlap duration.
For outward adaptation neither the duration increase nor the peak velocity depended on the overlap duration.

**Conclusion**

Our study highlights a number of differences between outward and inward saccadic adaptation. Outward adaptation transfers stronger from reactive to scanning and overlap saccades than inward adaptation. The transfer rate depends on the duration of the overlap, suggesting that the main factor is the length of integration time of the visual target signal. The transfer of outward adaptation is driven by a duration increase that occurs for the adapted and all other saccade categories. The transfer of inward adaptation, on the other hand, relies on a decrease of peak velocity which occurs for the adapted and all other saccade categories. The duration decrease seen in the adapted reactive saccade does not transfer to the other saccade categories, suggesting that two factors are involved in inward adaptation but only one is general for all saccade types.
Grants

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References


Figure legends

Figure 1:

Course of experimental sessions in testing adaptation transfer from reactive saccades to other saccade categories. White squares with symbols indicate all test saccades (plus sign = reactive, empty circle = gap, filled circle = overlap, filled triangle = scanning, empty triangle = memory-guided). Black rectangles indicate reactive target-on saccades. Experiments were divided into three phases. I: pre-adaptation phase (250 trials), II: adaptation-phase (300 trials), III: post-adaptation phase (250 trials). Experimental sessions were either with inward adaptation or with outward adaptation. Pre- and post-adaptation phases were divided in blocks, each with one type of test saccade. 5 test saccades within a block were separated by 10 reactive target-on saccades. 5 test saccades in between blocks were separated by 15 reactive target-on saccades. To prevent from an effect of order, blocks were randomized in each experimental session.

Figure 2:

A: Example for the time course of saccadic inward adaptation in the first experiment. B: Example for the time course of saccadic outward adaptation in the first experiment. The crosses indicate the reactive trials. The mean saccade amplitudes of these latter trials in the pre- and post adaptation phases is given by the horizontal gray rectangles. Their thickness indicates twice the standard error. Plus signs indicate reactive test trials. Empty circles indicate gap test trials. Filled circles indicate overlap test trials. Filled triangles indicate scanning test trials. Empty triangles indicate memory-guided test trials.

Figure 3:

Mean amplitudes in the pre- and post-adaptation phases of the first experiment. A: Inward adaptation. B: Outward adaptation. Horizontal gray rectangles indicate the adapted reactive saccades (higher opacity: pre, lower opacity: post). Thickness of those rectangles indicates twice the standard error. Two neighbouring bars belong together, indicating mean amplitudes of a particular saccade type in pre- and post-adaptation phases, respectively (dark-gray: pre, light-gray: post). Error bars are standard errors.
**Figure 4:**

Percent Gain Transfer (PGT) for all test conditions of the first experiment. **A:** Inward adaptation. **B:** Outward adaptation. The PGT is computed in relation to the adapted reactive saccades. Error bars are standard errors. Significant PGT differences are observable between the overlap conditions and between the scanning conditions.

**Figure 5:**

Mean durations (dark-gray: pre, light-gray: post) of all tested saccade types of the first experiment. **A:** Inward adaptation. **B:** Outward adaptation. Mean peak velocities (dark-gray: pre, light-gray: post) of all tested saccade types of the first experiment. **C:** Inward adaptation. **D:** Outward adaptation. Horizontal gray rectangles indicate the reactive target-on trials (higher opacity: pre, lower opacity: post). Thickness of those rectangles indicates twice the standard error. Error bars are standard errors.

**Figure 6:**

**A:** Example for the time course of saccadic inward adaptation in the second experiment. Open circles indicate amplitudes of overlap test trials. **B:** Example for the time course of saccadic outward adaptation in the second experiment. Open triangles indicate amplitudes of overlap test trials. The crosses indicate amplitudes of reactive trials. The mean saccade amplitudes of these latter trials in the pre- and post adaptation phases is given by the horizontal gray rectangles. Their thickness indicates twice the standard error.

**Figure 7:**

Percental gain transfer (PGT) from reactive saccades to overlap saccades with a particular period of overlap. Open circles indicate the inward adaptation experiment. Open triangles indicate the outward adaptation experiment. Error bars are standard errors.
Figure 8:

Influence of saccadic inward adaptation of reactive saccades on the mean duration of overlap saccades with different periods of overlap. Error bars are standard errors.
Table 1:

Saccade parameters in all tested saccade conditions before and after saccadic inward and outward adaptation (first experiment).
pre-adaptation phase (without target displacement)

adaptation procedure (with target displacement)

post-adaptation phase (with target displacement)

test saccades (target off):

= reactive  = gap  = overlap  = scanning  = memory-guided
AB
reactive
gap
overlap
scanning
memory-guided

PGT in %

A

B

significant
\[ \triangle = \text{outward} \]
\[ \circ = \text{inward} \]
## Inward

<table>
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<th></th>
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<th>gain in %</th>
<th>latency in ms</th>
<th>duration in ms</th>
<th>peak velocity in deg/s</th>
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<td>Inward Reactive</td>
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<td>66.3±1.6</td>
<td>385±12</td>
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<td>Memory</td>
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<td>257.7±10.8</td>
<td>81.9±3.6</td>
<td>372±7</td>
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Values are means ± SE, paired t-tests were used for testing significance (* p<0.05, ** p<0.005, *** p<0.0005)

## Outward

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<th>latency in ms</th>
<th>duration in ms</th>
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<td>82.5±4.8</td>
<td>389±9</td>
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Values are means ± SE, paired t-tests were used for testing significance (* p<0.05, ** p<0.005, *** p<0.0005)