J Neurophysiol 106: 1399–1410, 2011.
First published June 15, 2011; doi:10.1152/jn.00236.2011.

Differences in intersaccadic adaptation transfer between inward and outward adaptation

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Submitted 16 March 2011; accepted in final form 7 June 2011

Schnier F, Lappe M. Differences in intersaccadic adaptation transfer between inward and outward adaptation. *J Neurophysiol* 106: 1399–1410, 2011. First published June 15, 2011; doi:10.1152/jn.00236.2011.—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.

saccade; adaptation; saccade dynamics; eye movements; learning

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 (Abel et al. 1978; Kommerell et al. 1976; 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 postsaccadic 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 (Collins et al. 2009; Havermann and Lappe 2010; Noto and Robinson 2001; Panouilleres et al. 2011; Shafer et al. 2000; Wallman and Fuchs 1998).

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 (Alahyane et al. 2008a; Collins et al. 2007; Frens and Van Opstal 1994; Noto et al. 1999; 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).

Nonmetric transfer, i.e., transfer when the metrics of adapted and test saccade are the same, occurs between saccades of different categories. 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 fixated 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 (FP). Whereas in scanning saccades both target and FP are constantly present, in memory-guided saccades the target is not visually available, and in reactive saccades the FP 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 FP, but the saccade is initiated only when the FP is turned off. For gap saccades, the FP 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 (Alahyane et al. 2007; Collins and Dore-Mazars 2006; Cotti et al. 2007; Deubel 1995; Deubel 1999; Erkelens and Hulleman 1993; Fujita et al. 2002; Gaveau et al. 2005; 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

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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 (Ethier et al. 2008; Fuchs et al. 1996; Miller et al. 1981; Panouilleres et al. 2009; Robinson et al. 2003; Scudder et al. 1998; Straube et al. 1997). Moreover, outward adaptation is less stable than inward adaptation, as shown by faster de-adaptation of the outward adapted state (Straube et al. 1997). Furthermore, inward adaptation leads to a decrease in saccadic peak velocity (Abrams et al. 1992; Fitzgibbon et al. 1985; Straube et al. 1995; Straube et al. 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 midflight 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 adaptation 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 (Schnier et al. 2010; Zimmermann and Lappe 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 (Collins et al. 2007; Frens and Van Opstal 1994; 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-in. monitor (Eizo FlexScan F930) with a vertical frequency of 120 Hz at a resolution of 1,024 × 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° × 30°.

Experiments were done in complete darkness with a background luminance <0.0006 cd/m^2. 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). Subjects had to perform all experimental sessions binocular, with only the left eye tracked. All data, including online events, raw gaze position samples (at 1,000 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°/s and an acceleration threshold of 4,000°/s^2.

Procedure for Reactive Saccade Adaptation

FP and target (T1) were red disks with a radius of 0.5° and a luminance of 0.13 cd/m^2. Both disks were clearly visible under photopic conditions [cf. Georg et al. (2008)]. At the beginning of each trial, FP was presented 12° to the left of the center of the screen. Correct fixation was checked online. After a variable time between 500 and 1,100 ms, the FP disappeared, and subjects had to perform a saccade toward the simultaneously appearing target T1, which was 8° to the right of the center of the screen. Saccade onset was detected online when the eye position was exceeding a 3° trigger threshold rightwards from the FP. At this time, the saccade target T1 stepped 6° inwards, or 6° 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. Five hundred fifty milliseconds 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 3° threshold rightwards from the FP.

Gap test saccades. Three hundred milliseconds after the subject had established fixation, the radius of FP was slowly decreased until FP completely vanished. This procedure took further 800 ms and should prevent subjects from falsely reacting on the extinction of the FP. Preliminary experiments had shown that, because the different task types were intermixed in each session, many subjects had difficulties in keeping fixation when the FP was turned off. In the reactive, overlap, and memory-guided tasks, the extinction of the FP coincided with the go signal of the saccade. We designed the gradual fading of the FP in our gap condition to help the subjects keep fixation and shield them from any unwanted reaction triggered by sudden FP offset. At a variable time between 400 and 1,000 ms after the FP had completely disappeared, the target T1 appeared, and subjects had to perform the saccade toward 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 FP. Second, there is the large and variable gap duration of between 400 and 1,000 ms, which was chosen to make our gap condition comparable to the overlap saccade condition. Most other studies used gaps of ~200 ms (Deubel 1999; Fuchs et al. 1996; Hopp and Fuchs 2010). Because of the difference in FP 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 1,100 ms, and correct fixation was checked. Then T1 was presented for 200 ms while subjects continuously fixated FP. After a variable time between 400 and 1,000 ms, FP disappeared, and subjects had to perform a saccade toward the remembered position of T1. One thousand fifty milliseconds after the saccade, the next trial began.

Overlap test saccades. In overlap trials, FP appeared for a variable time between 500 and 1,100 ms, and correct fixation was checked. Then T1 appeared together with FP for a variable time between 400 and 1,000 ms, indicating the overlap duration. Thereafter, FP disappeared, and subjects had to perform a saccade toward T1. After saccade onset, i.e., when eye position exceeded a 3° threshold rightwards from the FP, T1 was extinguished.

In the second experiment of this study, overlap test saccades were measured with seven different overlap durations, i.e., 0, 150, 250, 400, 700, 1,400, and 2,500 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° above T1 and FP, respectively. Therefore, the four targets formed a rectangle of width 20° and height 12°. 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 3° threshold leftwards from A, and B disappeared when eye position exceeded a 3° threshold downwards from B. During the last saccade, the saccade from FP to T1, T1 also disappeared when eye position exceeded a 3° threshold rightwards from the FP.

Course of the Experiments

An experimental session of the first experiment consisted of 250 preadaptation trials, 300 adaptation trials, and 250 postadaptation trials. Preadaptation phase and postadaptation 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 Fig. 1). Reinforcing reactive saccades were without the target step from T1 to T2 in the preadaptation phase, but with this target step in the postadaptation 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 postadaptation 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° 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 preadaptation trials, 300 adaptation trials, and 210 postadaptation trials. Adaptation trials were identical to those of the first experiment. The pre- and postadaptation 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, 150, 250, 400, 700, 1,400, or 2,500 ms) were

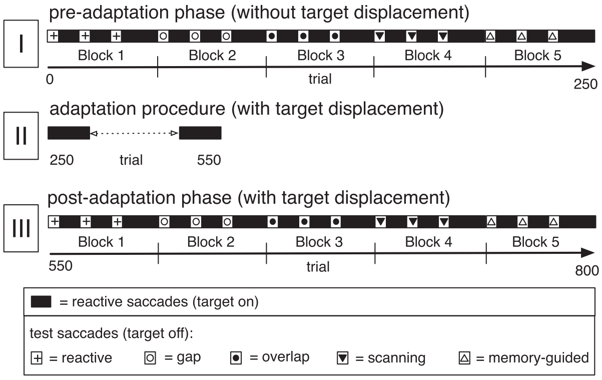

Fig. 1. Course of experimental sessions in testing adaptation transfer from reactive saccades to other saccade categories. White squares with symbols indicate all test saccades (plus sign = reactive, empty circle = gap, filled circle = overlap, filled triangle = scanning, empty triangle = memory guided). Black rectangles indicate reactive target-on saccades. Experiments were divided into three phases: I: preadaptation phase (250 trials); II: adaptation phase (300 trials); and III: postadaptation phase (250 trials). Experimental sessions were either with inward adaptation or with outward adaptation. Pre- and postadaptation phases were divided in blocks, each with one type of test saccade. Five test saccades within a block were separated by 10 reactive target-on saccades. Five 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.

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 postadaptation phases in each session. Each subject completed four sessions in random order: two experimental sessions with inward adaptation and two with outward adaptation.

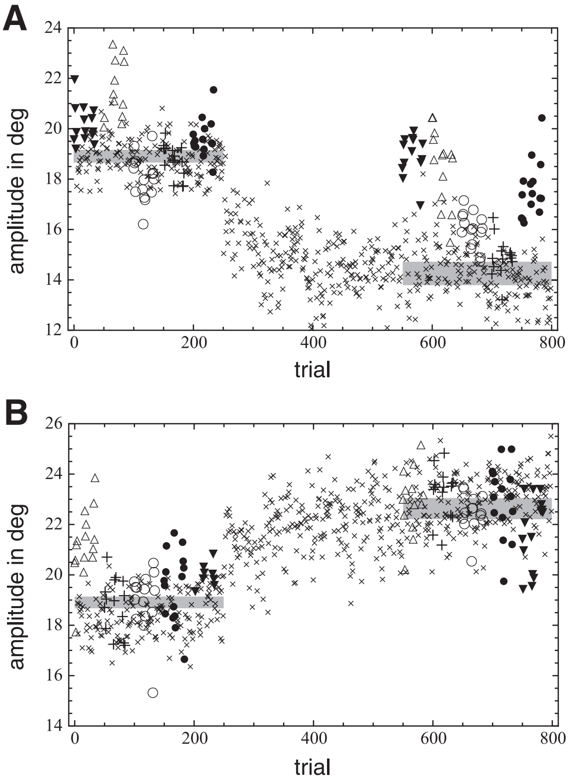

Fig. 2. *A*: example for the time course of saccadic inward adaptation in the first experiment. *B*: example for the time course of saccadic outward adaptation in the first experiment. The crosses indicate the reactive trials. The mean saccade amplitudes of these latter trials in the pre- and postadaptation phases are given by the horizontal gray rectangles. Their thickness indicates twice the SE. 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.

Participants

Eight subjects (2 women, 6 men, 1 author, 7 naïve; age range: 21–38 yr) participated in all experimental sessions of the first experiment, 19 subjects (12 women, 7 men, 1 author, 18 naïve; age range: 20–38 yr) in all experimental sessions of the second. Six subjects of the first experiment also participated in the second experiment (2 women, 4 men, 1 author, 5 naïve; age range: 21–38 yr). Two subjects (2 women, 22 and 25 yr) 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 and the guidelines of the local ethics committee (Department of Psychology, University of Muenster, Germany), which approved this study.

Data Analysis

Mathematica 7.0 was used for all data analysis. Except for the scanning condition, the 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° diameter around the FP, its amplitude had to be between 10 and 30°, 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 1,000 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 postadaptation phase and calculating the gain change in each saccade condition according to

$$\text{gain change\%} = (\text{amplitude}_{\text{post}} - \text{amplitude}_{\text{pre}})/\text{amplitude}_{\text{pre}} \cdot 100$$

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 neighboring 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 shows example sessions for inward and outward adaptation. The black crosses give the amplitudes of reactive saccades in the preadaptation, adaptation, and postadaptation 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 postadaptation test phase differed between saccade categories.

Adaptation. Averaged over all subjects, the mean amplitude of reactive saccades in the preadaptation phase was 18.91 ± 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° saccades with a ±6° step size is ±30%). The gain change was significantly lower in the outward compared with the inward adaptation (paired *t*-test with absolute values, $P < 0.0005$). During inward adaptation, mean latency increased from 195.7 ± 2.6 (SE) to 217.3 ± 4.8 (SE) ms (paired *t*-test, $P < 0.0005$), mean duration decreased from 66.1 ± 1.2 (SE) to 60.7 ± 1.6 (SE) ms (paired *t*-test, $P < 0.005$), and mean peak velocity decreased from 473 ± 16 (SE) to 397 ± 14°/s (SE) (paired *t*-test, $P < 0.0005$).

During outward adaptation, mean latency increased from 196.0 ± 1.9 (SE) to 205.3 ± 3.0 (SE) ms (paired *t*-test,

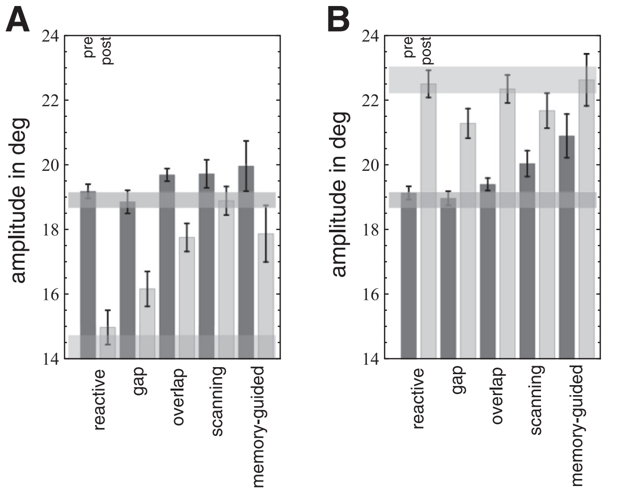

Fig. 3. Mean amplitudes in the pre- and postadaptation phases of the first experiment. *A*: inward adaptation. *B*: outward adaptation. Horizontal gray rectangles indicate the adapted reactive saccades (higher opacity: pre; lower opacity: post). Thickness of those rectangles indicates twice the SE. Two neighboring bars belong together, indicating mean amplitudes of a particular saccade type in pre- and postadaptation phases, respectively (dark gray: pre; light gray: post). Error bars are SEs.

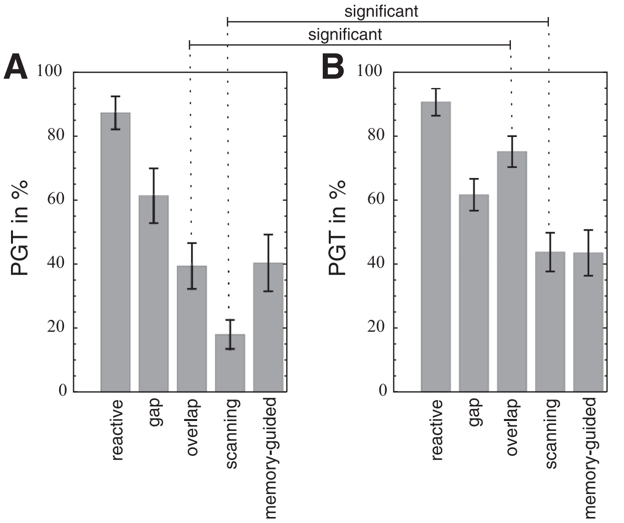

Fig. 4. Percent gain transfer (PGT) for all test conditions of the first experiment. *A*: inward adaptation. *B*: outward adaptation. The PGT is computed in relation to the adapted reactive saccades. Error bars are SEs. Significant PGT differences are observable between the overlap conditions and between the scanning conditions.

$P < 0.05$), and mean duration increased from 65.8 ± 1.4 (SE) to 73.4 ± 0.9 (SE) ms (paired *t*-test, $P < 0.0005$). Mean peak velocity remained almost constant [Pre: 476 ± 9°/s (SE), Post: 485 ± 11°/s (SE) (paired *t*-test, $P = 0.14$)].

Transfer. Figure 3 shows the mean amplitudes of all test saccade types in the pre- and postadaptation phases. In the preadaptation 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 ~1°, those of overlap, scanning, and memory-guided test saccades ~0.3° 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 between 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

Table 1. *Saccade parameters in all tested saccade conditions before and after saccadic inward and outward adaptation (first experiment)*

	Amplitude, °				Latency, ms			Duration, ms			Peak Velocity, °/s		
	Pre	Post	Sig.	Gain, %	Pre	Post	Sig.	Pre	Post	Sig.	Pre	Post	Sig.
Inward													
Reactive	19.18 ± 0.22	14.98 ± 0.53	***	−21.9 ± 2.5	194.4 ± 4.4	224.6 ± 7.8	**	66.5 ± 1.4	61.8 ± 1.8	**	483 ± 12	408 ± 17	***
Gap	18.86 ± 0.35	16.17 ± 0.54	***	−14.4 ± 1.7	266.6 ± 14.6	261.8 ± 9.0	NS	66.1 ± 1.2	68.2 ± 2.1	*	466 ± 12	406 ± 20	***
Overlap	19.69 ± 0.20	17.76 ± 0.43	***	−9.8 ± 1.9	235.2 ± 7.6	255.6 ± 10.0	*	70.7 ± 1.9	72.3 ± 1.5	NS	449 ± 16	392 ± 14	**
Scanning	19.72 ± 0.43	18.89 ± 0.44	**	−4.1 ± 1.1	389.6 ± 45.8	390.6 ± 47.5	NS	66.3 ± 1.6	70.2 ± 2.1	*	485 ± 12	453 ± 17	*
Memory	19.96 ± 0.78	17.87 ± 0.87	***	−10.5 ± 2.7	257.7 ± 10.8	275.1 ± 13.0	*	81.8 ± 3.6	85.0 ± 3.5	NS	372 ± 7	328 ± 16	*
Outward													
Reactive	19.13 ± 0.20	22.50 ± 0.42	***	17.6 ± 1.5	192.6 ± 5.5	210.9 ± 5.7	**	68.4 ± 2.1	73.9 ± 0.8	**	483 ± 10	474 ± 11	NS
Gap	18.97 ± 0.22	21.28 ± 0.46	***	12.2 ± 1.5	266.1 ± 9.1	258.4 ± 9.9	NS	66.4 ± 1.6	72.3 ± 1.2	***	477 ± 5	469 ± 8	NS
Overlap	19.40 ± 0.19	22.34 ± 0.43	***	15.2 ± 1.8	234.5 ± 10.5	261.9 ± 14.5	*	69.4 ± 1.3	78.1 ± 1.1	***	448 ± 8	443 ± 14	NS
Scanning	20.04 ± 0.40	21.67 ± 0.54	***	8.1 ± 1.0	385.7 ± 36.9	394.1 ± 45.4	NS	66.0 ± 1.5	71.4 ± 1.7	**	497 ± 11	481 ± 12	*
Memory	20.89 ± 0.68	22.63 ± 0.89	***	8.3 ± 1.4	288.6 ± 23.3	273.0 ± 15.0	NS	82.5 ± 4.8	88.1 ± 3.9	**	389 ± 9	384 ± 11	NS

Values are means ± SE. Pre and Post: before and after, respectively, saccadic inward and outward adaptation. Paired *t*-tests were used for testing significance (Sig.): $^{*}P < 0.05$, $^{**}P < 0.005$, $^{***}P < 0.0005$. NS, nonsignificant.

$$\text{PGT} = \text{gain change\% (tested)} / \text{gain change\% (adapted)} \cdot 100$$

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 (Fig. 4*A*), 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 that 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 (Fig. 4*B*), 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 $\sim$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 five 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 compared with the reactive saccade.

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 compared with 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 postadaptation phase, the mean duration of reactive

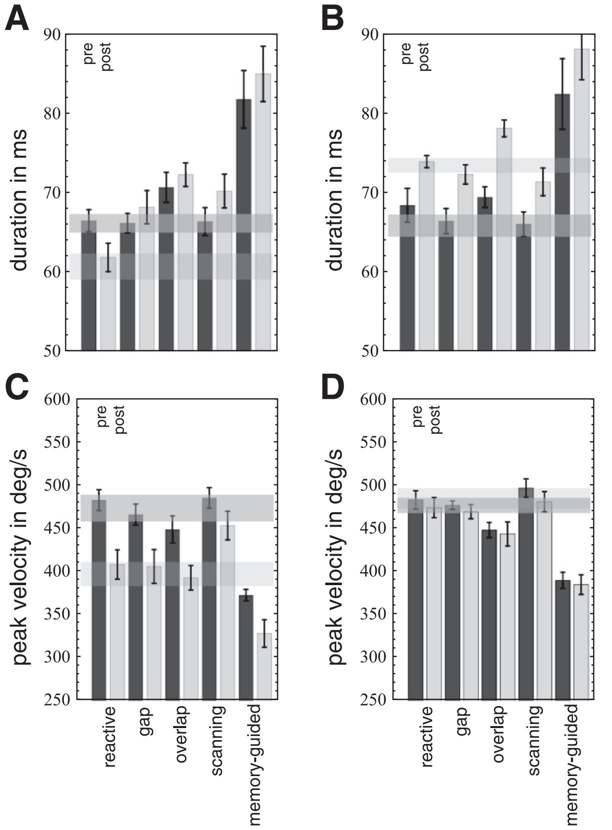

Fig. 5. Mean durations (dark gray: pre; light gray: post) are shown of all tested saccade types of the first experiment for inward adaptation (*A*) and outward adaptation (*B*). Mean peak velocities (dark gray: pre; light gray: post) are shown of all tested saccade types of the first experiment for inward adaptation (*C*) and outward adaptation (*D*). Horizontal gray rectangles indicate the reactive target-on trials (higher opacity: pre; lower opacity: post). Thickness of those rectangles indicates twice the SE. Error bars are SEs.

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 that 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.

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 internally (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 FP. 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 between 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 increasing 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 condition. 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 varying 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 postadaptation phases, overlap saccades with seven different overlap durations were tested: 0, 150, 250, 400, 700, 1,400, or 2,500 ms. These overlap saccades were tested in blocks of 5, interspersed with 10 reinforcing reactive saccades. Note that the 0-ms overlap condition is identical to the reactive saccade condition, only that it was announced by the computer voice as an overlap block.

Saccade parameters in the preadaptation phase. Because our paradigm combined trials of overlap saccades with different overlap duration, we analyzed saccade amplitudes in the preadaptation 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 ± 0.19° (SE), or 0.25° below the target amplitude of 20°. At 400 ms overlap, mean saccade amplitude was 19.96 ± 0.19° (SE), or 0.04° below target amplitude. For even longer overlap duration, accuracy dropped again. At 2,500 ms overlap, mean saccade amplitude was 19.62 ± 0.24° (SE), or 0.38° 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 ± 0.9 (SE) ms at 0-ms overlap to 72.2 ± 2.2 (SE) ms at 2,500-ms overlap. Peak velocity decreased with increasing overlap from 504 ± 10°/s (SE) at 0-ms overlap to 460 ± 10°/s (SE) at 2,500-ms overlap. The increase of duration and decrease of peak velocity were 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 postadaptation test phases (Fig. 6) differed between different overlap test conditions.

Averaged over all subjects, the mean saccadic amplitude decreased during inward adaptation from 19.40 ± 0.17° (SE) to 14.55 ± 0.28° (SE), which corresponds to a gain decrease of −25.1 ± 1.0% (SE) (expected maximum gain change for 20° saccades with a −6° step size is −30%). During outward adaptation, the mean saccadic amplitude increased from 19.34 ± 0.15° (SE) to 22.94 ± 0.22° (SE), which corresponds to a gain increase of 18.6 ± 0.9% (SE) (expected maximum gain change for 20° saccades with a 6° step size is 30%). The gain change

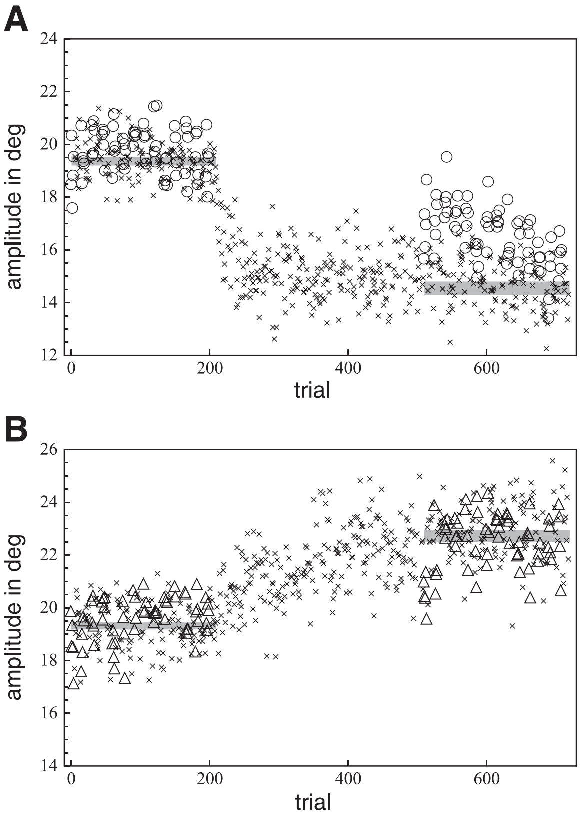

Fig. 6. *A*: example for the time course of saccadic inward adaptation in the second experiment. Open circles indicate amplitudes of overlap test trials. *B*: example for the time course of saccadic outward adaptation in the second experiment. Open triangles indicate amplitudes of overlap test trials. The crosses indicate amplitudes of reactive trials. The mean saccade amplitudes of these latter trials in the pre- and postadaptation phases are given by the horizontal gray rectangles. Their thickness indicates twice the SE.

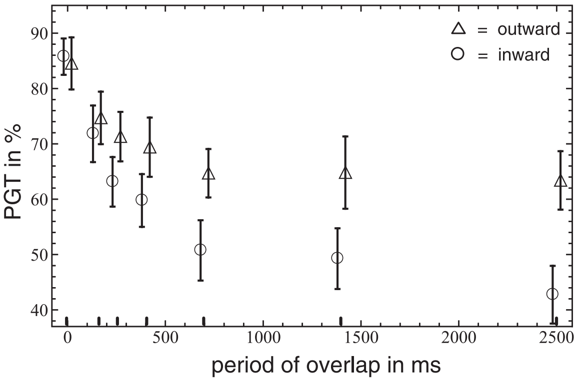

Fig. 7. PGT from reactive saccades to overlap saccades with a particular period of overlap. Open circles indicate the inward adaptation experiment. Open triangles indicate the outward adaptation experiment. Error bars are SEs.

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 ± 3.9 to 210.8 ± 3.8 (SE) ms (paired *t*-test, $P < 0.0005$), mean duration decreased from 66.2 ± 0.8 to 59.2 ± 0.8 (SE) ms (paired *t*-test, $P < 0.0005$), and mean peak velocity decreased from 499 ± 10 to 432 ± 14°/s (SE) (paired *t*-test, $P < 0.0005$).

During outward adaptation, mean latency increased from 201.8 ± 2.9 to 209.9 ± 2.8 (SE) ms (paired *t*-test, $P < 0.0005$), mean duration increased from 66.7 ± 1.1 to 77.3 ± 1.8 (SE) ms (paired *t*-test, $P < 0.0005$), and mean peak velocity remained constant [Pre: 503 ± 10°/s (SE), Post: 500 ± 12°/s (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 shows the PGT for each overlap test condition. PGT was high for short overlap durations. As in the first experiment of this study, the PGT to overlap test saccades with 0-ms period of overlap, i.e., reactive test saccades, was not 100%, but only ~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 transferred to 43 ± 5% (SE) to overlap saccades with 2,500-ms period of overlap, outward adaptation transferred to 63 ± 5% (SE). Our observations were supported by a two-way repeated-measures ANOVA with the factors overlap duration (0, 150, 250, 250, 400, 700, 1,400, 2,500 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 ± 5.3 (SE) ms at 0-ms overlap to 242.5 ± 7.1 (SE) ms at 2,500-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 ± 2.7 (SE) ms, $P < 0.005$; mean increase after outward adaptation: 8.2 ± 2.1 (SE) ms, $P < 0.005$], 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 vs. saccade amplitudes before adaptation and linear regressions of latencies vs. 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°/ms. The same applied to linear regressions of binned latencies vs. binned difference between postadaptation amplitudes and preadaptation 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 ± 0.9 (SE) ms (*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 ± 0.8 (SE) ms at 2,500-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. Fig. 8). Inward adaptation diminished peak velocities in the same manner as the mean peak velocity of the adapted saccade itself, on average by ~60°/s, independent of the overlap duration [ANOVA, $F(6,96) = 1.11$, $P = 0.36$].

Outward adaptation increased mean duration by ~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

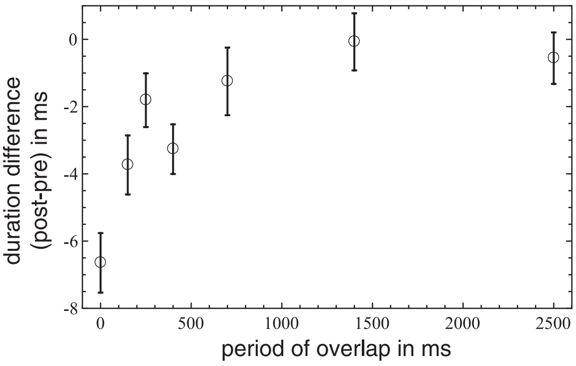

Fig. 8. Influence of saccadic inward adaptation of reactive saccades on the mean duration of overlap saccades with different periods of overlap. Error bars are SEs.

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.

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 (Ethier et al. 2008; Fuchs et al. 1996; Miller et al. 1981; Panouilleres et al. 2009; Robinson et al. 2003; Scudder et al. 1998; Straube and Deubel 1995; Straube et al. 1997). Outward and inward adaptation affect saccade dynamics differently. Saccades after saccadic outward adaptation have similar dynamics as nonadapted saccades of the same amplitude, whereas saccades after inward adaptation show decreased peak velocity (Abrams et al. 1992; Chen-Harris et al. 2008; Ethier et al. 2008; Fitzgibbon et al. 1985; Straube et al. 1995, Straube et al. 1997).

Outward adaptation shows a stronger transfer to perception (Schnier et al. 2010; Zimmermann and Lappe 2010) and hand pointing (Hernandez et al. 2008) than inward adaptation and a different pattern of transfer to other saccade amplitudes (Collins et al. 2007; Schnier et al. 2010; Semmlow et al. 1989). 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 (Alahyane et al. 2007; Collins and Dore-Mazars 2006; Cotti et al. 2009; Deubel 1999; Erkelens and Hulleman 1993; Fujita et al. 2002; Hopp and Fuchs 2010; Zimmermann and Lappe 2009). 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 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 voluntary and reactive saccades, while partially overlapping loci at higher levels are specific to each saccade type. These more specific loci might involve various areas of the oculomotor pathways, such as the brain stem, cerebellum, or thalamocortical circuits, some of which are closer to the motor side of saccade performance and some closer to visual target registration and movement planning (Alahyane et al. 2008b; Gaymard et al. 2001; Hopp and Fuchs 2002; MacAskill et al. 2002; 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 neuronal 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 saccades 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 transformations, and that perception should be unaffected after both adaptation methods. This, however, disagrees with studies, which revealed adaptation transfer to perception (Schnier et al. 2010; Zimmermann and Lappe 2010) and hand-pointing (Hernandez et al. 2008) after outward adaptation and suggested that outward 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 paradigm. 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 central nervous system. 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 differences 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 inward 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 preadaptation 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 (Dorris and Munoz 1998; Paré and Munoz 1996; Rolfs and Vitu 2007). 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 nonadapted 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 ~30°/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

M. Lappe is supported by the German Science Foundation DFGLA-952/3 and DFG LA-952/4, the German Federal Ministry of Education and Research project Visuo-Spatial Cognition, and the EC Project Eyeshots.

DISCLOSURES

No conflicts of interest (financial or otherwise) are declared by the author(s).

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