J Neurophysiol 107: 3062–3070, 2012.
First published March 21, 2012; doi:10.1152/jn.00877.2011.

Mislocalization of stationary and flashed bars after saccadic inward and outward adaptation of reactive saccades

Fabian Schnier and Markus Lappe
Institute of Psychology and Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, University of Muenster, Münster, Germany

Submitted 27 September 2011; accepted in final form 15 March 2012

Schnier F, Lappe M. Mislocalization of stationary and flashed bars after saccadic inward and outward adaptation of reactive saccades. *J Neurophysiol* 107: 3062–3070, 2012. First published March 21, 2012; doi:10.1152/jn.00877.2011.—Recent studies have shown that saccadic inward adaptation (i.e., the shortening of saccade amplitude) and saccadic outward adaptation (i.e., the lengthening of saccade amplitude) rely on partially different neuronal mechanisms. There is increasing evidence that these differences are based on differences at the target registration or planning stages since outward but not inward adaptation transfers to hand-pointing and perceptual localization of flashed targets. Furthermore, the transfer of reactive saccade adaptation to long-duration overlap and scanning saccades is stronger after saccadic outward adaptation than that after saccadic inward adaptation, suggesting that modulated target registration stages during outward adaptation are increasingly used in the execution of saccades when the saccade target is visually available for a longer time. The difference in target presentation duration between reactive and scanning saccades is also linked to a difference in perceptual localization of different targets. Flashed targets are mislocalized after inward adaptation of reactive and scanning saccades but targets that are presented for a longer time (stationary targets) are mislocalized stronger after scanning than after reactive saccades. This link between perceptual localization and adaptation specificity suggests that mislocalization of stationary bars should be higher after outward than that after inward adaptation of reactive saccades. In the present study we test this prediction. We show that the relative amount of mislocalization of stationary versus flashed bars is higher after outward than that after inward adaptation of reactive saccades. Furthermore, during fixation stationary and flashed bars were mislocalized after outward but not after inward adaptation. Thus, our results give further evidence for different adaptation mechanisms between inward and outward adaptation and harmonize some recent research.

saccade; eye movements; visual localization

CLEAR VISION IS BASED on the ability to make saccades as accurately as possible. Accuracy of the saccadic system is maintained by the mechanism of saccadic adaptation. Saccadic inaccuracies may occur as a consequence of eye muscle weakness (Abel et al. 1978; Kommerell et al. 1976; Optican et al. 1985), but may also be artificially generated and studied in the laboratory by a systematic intrasaccadic displacement of the saccade target (McLaughlin 1967; Miller et al. 1981). The resulting difference between the eye landing position and the postsaccadic visual location of the target induces the adjustment of transformation parameters between the visual input and the motor commands. This adjustment reduces the postsaccadic visual error during subsequent trials and allows the eyes to land closer to the shifted target. The effectiveness of saccadic adaptation depends on the location, timing, and consistency of the postsaccadic error (Collins et al. 2009; Havermann and Lappe 2010; Noto and Robinson 2001; Panouilleres et al. 2011; Shafer et al. 2000; Wallman and Fuchs 1998; Zimmermann and Lappe 2010).

Saccadic adaptation is specific to the direction and amplitude of the saccade (Albano and King 1989; Collins et al. 2007; Deubel 1987; Deubel et al. 1986; Frens and Van Opstal 1994; Schnier et al. 2010), to the initial eye position (Havermann et al. 2011; Zimmermann and Lappe 2011), and to the particular saccade type.

Saccade types can be distinguished by the way the saccade is triggered. Reactive saccades are elicited by a sudden appearance of a saccade target and simultaneous disappearance of the fixation point (Deubel 1995; Hopp and Fuchs 2004). Because there is only limited time to integrate spatiotemporal target information, reactive saccades are thought to receive target localization signals from comparatively early visual areas in the oculomotor pathway (Gaymard et al. 2003; Müri and Nyffeler 2008; Pierrot-Deseilligny 1991). During overlap saccades, on the other hand, the fixation point and the saccade target are presented simultaneously for a certain period of time and the saccade is initiated when the fixation point turns off (Deubel 1995; Hopp and Fuchs 2004). Because there is more time to integrate spatiotemporal target information overlap saccades might receive target localization signals from higher visual areas in the oculomotor pathway (Deubel 1999; Müri and Nyffeler 2008; Rivaud et al. 1994). The same would apply to scanning saccades, which are self-paced and internally triggered saccades within a continuously present scene, and thus do not contain trigger signals for saccade execution (Deubel 1995; Hopp and Fuchs 2004).

Many transfer studies revealed that adaptation transfer differs between these different saccade types and is often not symmetric (reviewed in Pélisson et al. 2010). There is a strong transfer from scanning to reactive saccades but a comparatively weak, though often significant, transfer in the opposite direction (Collins and Doré-Mazars 2006; Cotti et al. 2007; Erkelens and Hulleman 1993; Fujita et al. 2002; Gaveau et al. 2005; Zimmermann and Lappe 2009). Because of the nonzero and asymmetric transfer one may argue for a common locus in the final common saccadic pathway, together with other adaptation loci that are more specific to each saccade category (Alahyane et al. 2007). Besides, differences in the temporal properties of the generation of reactive and scanning saccades may lead to asymmetric transfer. Reactive saccades have shorter latencies

---

Address for reprint requests and other correspondence: M. Lappe, Institute of Psychology and Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, Univ. of Muenster, Fliednerstraße 21, 48149 Münster, Germany (e-mail: mlappe@uni-muenster.de).

than those of scanning saccades, and are thus presumably driven by neurons with short latencies and limited temporal integration. Thus, adaptation of reactive saccades should lead to only minor adaptation of scanning saccades since scanning saccades presumably involve both short-latency and long-latency neurons. Scanning saccade adaptation, in contrast, should lead to clear adaptation of reactive saccades since both involve short-latency neurons. Indeed, the amount of transfer between reactive and overlap saccades depends on the duration of the overlap (Deubel 1999; Schnier and Lappe 2011).

Saccadic adaptation not only influences saccade amplitudes but also visual localization. This pertains to the perception of visual targets flashed before an adapted saccade (Awater et al. 2005; Bruno and Morrone 2007; Collins et al. 2007; Georg and Lappe 2009; Schnier et al. 2010), the pointing to a flashed target with the hand (Bruno and Morrone 2007; Cotti et al. 2007, 2009; Hernandez et al. 2008; but see Cecala and Freedman 2008, 2009; Kroller et al. 1996; McLaughlin et al. 1968), and even the apparent position of the saccade target itself (Bahcall and Kowler 1999). The strength of mislocalization depends on the saccade type, but also on the properties of the target. Zimmermann and Lappe (2009) investigated changes in visual localization of stationary (i.e., long visible) and flashed (i.e., short visible) bars after adaptive shortening of reactive and scanning saccades. They observed that briefly presented localization probes were mislocalized after adaptation of both saccade types, whereas stationary localization probes were mislocalized only after adaptation of scanning saccades. Since flashed probes resemble a potential target for reactive saccades and stationary probes resemble a potential target for scanning saccades the observed asymmetry of visual localization resembles the asymmetry of transfer behavior between reactive and scanning saccades (Alahyane et al. 2007; Collins and Doré-Mazars 2006; Cotti et al. 2007; Deubel 1999; Pélisson et al. 2010). The link may lie in the temporal properties of target localization and saccade generation, involving short-latency neurons for reactive saccades and flashed probes and short-plus long-latency neurons for scanning saccades and stationary probes. In this view, one may argue that localization judgments and saccade targeting share a common representation. This is also supported by findings that mislocalization also occurs during periods of fixation (Garaas and Pomplun 2011; Moidell and Bedell 1988; Schnier et al. 2010; Zimmermann and Lappe 2010), suggesting that saccadic adaptation affects visual localization at the target registration or planning stages.

There is a second factor that divides saccadic adaptation properties, that is, the distinctions between inward (or amplitude shortening) and outward (or amplitude lengthening) adaptation. Saccade amplitude is lengthened when the saccade target is shifted in the primary saccade direction. Saccade amplitude is shortened when the target is shifted against the primary saccade direction. Many studies revealed differences between inward and outward adaptation (reviewed in Pélisson et al. 2010). For example, more trials with target displacement are required to reach a steady adaptation state during outward adaptation than during inward adaptation. Furthermore, the corresponding final gain level is lower and less stable after outward adaptation than after inward adaptation (Ethier et al. 2008; Golla et al. 2008; Hernandez et al. 2008; Miller et al. 1981; Panouilleres et al. 2009; Schnier and Lappe 2011; Semmlow et al. 1989; Straube and Deubel 1995; Straube et al. 1997; Zimmermann and Lappe 2010). Finally, differences have also been observed in the adjustment of saccade dynamics (peak velocity, duration) between the inward and outward adaptation procedures (Ethier et al. 2008; Golla et al. 2008; Schnier and Lappe 2011).

Transfer from reactive saccades to overlap and scanning saccades is significantly stronger after outward adaptation than that after inward adaptation (Schnier and Lappe 2011). Such a transfer difference was not found for the gap and the memory-guided saccade type, suggesting that the amount by which gain transfer differed between inward and outward adaptation for scanning and overlap saccades seems to be essentially related to the presentation duration of the saccade target.

The above-mentioned studies on visual localization after saccadic adaptation also support differences between inward and outward adaptation. Hernandez et al. (2008) found changes in hand-pointing direction after outward adaptation, but not after inward adaptation. Zimmermann and Lappe (2010) showed that visual localization of eccentric targets during fixation was much more susceptible to saccadic adaptation for outward than for inward adaptation. These results, together with those of Schnier and Lappe (2011) and Ethier et al. (2008), suggest that there is a stronger modulation of target localization stages after outward than that after inward adaptation of reactive saccades. In this view, target localization stages, located before the sensorimotor transformation, are especially used in the execution of overlap and scanning saccades, leading to a higher amount of transfer to these latter saccade types dependent on whether target localization stages are modulated by saccadic adaptation. This in turn implies that target localization for the execution of reactive saccades may be partially different from that of overlap or scanning saccades because there is less time to integrate spatiotemporal target information.

Since there is a stronger adaptation transfer from reactive to long-duration overlap or scanning saccades after outward than after inward adaptation of reactive saccades (Schnier and Lappe 2011), we wondered whether the mislocalization of stationary probes that was observed for inward adaptation of scanning but not reactive saccades (Zimmermann and Lappe 2009), reflecting the asymmetric transfer behavior between both saccade types, may be observed for reactive saccades when outward rather than inward adaptation is performed. In this context we also tested the adaptation-induced localization judgments of flashed and stationary bars during periods of fixation. If outward adaptation of reactive saccades affects target localization stages that are also used for saccades with a longer target presentation duration, as for example scanning saccades, and adaptation of these latter saccade types affects target localization stages as shown by the adaptation-induced mislocalization during periods of fixation (Cotti et al. 2007, 2009), we wondered whether outward adaptation of reactive saccades induces mislocalization of flashed but also stationary bars during periods of fixation.

METHODS

Experimental Settings

Stimuli were presented on a 21-inch 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 supported by a 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. This low luminance was chosen to remove all visible background stimulation and particularly the borders of the monitor screen, which otherwise could provide visual references. Additionally, the monitor was covered with a dark foil that reduced the luminance by about two log units to prevent effects of phosphor persistence of the monitor. Nevertheless, all stimuli presented in this experiment were clearly visible under photopic conditions (for a detailed description, see Georg et al. 2008).

Eye Movement Recording

Eye movements were recorded with an EyeLink 1000 eye tracker (Desktop Mount Base System, SR Research Ltd., Mississauga, Ontario, Canada) using signals from the pupil and the corneal reflex. The recorded data comprised online events and raw gaze position samples (at 1,000 Hz) from the tracked left eye. 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. Messages were written into the eyelink file to structure and organize this file corresponding to the course of the program. Those messages include all necessary program information. Each eyelink file from each experimental session was offline checked for drifts that might have occurred. No drifts were detected.

Participants

Thirteen subjects (5 females, 8 males, 1 author, 12 naive, age range: 23–38 years) participated in this study. All of them had normal or corrected-to-normal vision and were experienced in eye movement experiments. Before starting the experiment participants gave informed consent in accordance with the Declaration of Helsinki and the guidelines of the ethics committee of the Department of Psychology, which approved this study.

Procedure for Reactive Saccade Adaptation

Fixation point (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. 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 300 and 700 ms 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 inducing a 20° reactive saccade. When eye position exceeded a 3° trigger threshold rightward from FP (saccade onset), the target T1 stepped 6° inward, or 6° outward to location T2 equivalent to a 30% inward or outward target step. The direction of the step (inward/outward) depended on the particular experimental session and never changed within each session. T2 remained visible for a further 500 ms. After a further 550 ms the next trial began.

Procedures for Test Localization Trials

At the beginning of each localization trial FP was presented 12° to the left of the center of the screen. Correct fixation was the trigger to proceed with the trial.

Localization judgments of stationary bars. A bar (width 0.3°, height 2°, and luminance 0.13 cd/m^2) was presented at a random position within a rectangular space (width 4°, height 2°) centered 2° directly above the target position T1. After a variable time between 800 and 1,200 ms the fixation point was extinguished and, simultaneously, the target T1 appeared. Subjects performed a saccade to T1. At saccade onset the bar was extinguished. The target remained visible for a further 500 ms. Thereafter a mouse pointer appeared at a random position 4° beyond the horizontal centerline of the screen and subjects had to indicate the perceived position of the stationary bar (cf. Fig. 1*A* for a timeline view). Thus, localization judgments were done on a completely dark stimulus screen without any visual references.

In some trials the target disappeared at saccade onset together with the bar. These target-off trials were introduced to remove any postsaccadic visual references that might affect the localization judgment. Accordingly, the trials in which the target remained visible after the saccade were named target-on trials.

Localization judgments of flashed bars. The FP remained visible for a variable time between 800 and 1,200 ms. Then, the fixation point was extinguished, the target T1 appeared, and subjects performed a saccade to T1. By 80 ms after the appearance of T1 and thus on average about 130 ms before saccade onset a bar was presented for 25 ms at a random position within a rectangular space (width 4°, height 2°), centered 2° directly above the target position T1. After saccade onset the target disappeared during target-off trials, or remained visible for a further 500 ms during target-on trials. Thereafter, a mouse pointer appeared at a random position 4° beyond the horizontal centerline of the screen. Subjects had to indicate the perceived

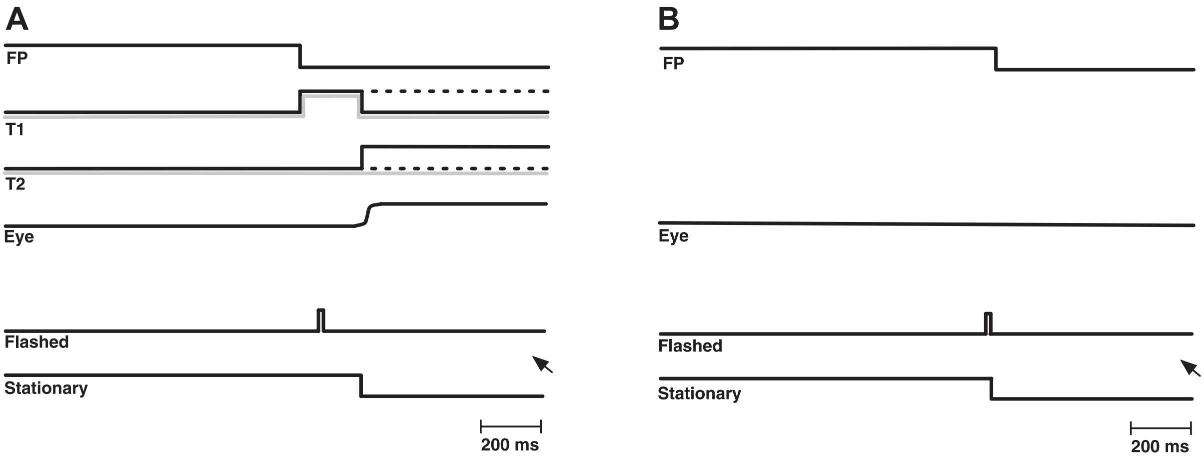

Fig. 1. Timelines of the trials for the localization judgments of stationary and flashed bars during saccades (*A*) and during fixation (*B*). The *solid black lines* in *A* for targets T1 and T2 indicate target-on trials in the postadaptation phase. The corresponding *dashed lines* indicate the timings in the preadaptation phase. The *solid gray lines* for T1 and T2 indicate target-off trials. T1 was 20° rightward from fixation point (FP). T2 appeared 6° leftward or rightward from T1, dependent on the experimental session (inward/outward). During fixation trials (*B*) a modified version of the FP (*circle*) and an additional computer voice reminded subjects not to perform a saccade but fixate at the circle. In all conditions the bar (width 0.3°, height 2°, luminance 0.13 cd/m^2) was presented at a random position within an area 4° wide, 2° high centered, 2° directly above the target position T1. Subjects had to indicate the perceived bar position with a mouse pointer.

position of the flashed bar (cf. Fig. 1*A* for a timeline view). Thus, localization judgments were done on a completely dark stimulus screen without any visual references.

Comparison between localization trials for the judgment of stationary bars and localization trials for the judgment of flashed bars reveals that both differed only in that in the former the localization bar was visible for 800 to 1,200 ms together with FP, whereas in the latter the bar was flashed for 25 ms after FP was turned off.

Localization judgments during fixation. In some trials, participants had to withhold the saccade and perform the visual localization while keeping fixation. A computer voice announced each fixation localization trial, and a modified FP, (i.e., a red circle with a radius of 0.5° and a thickness of 0.1°) reminded subjects to keep fixation during the following trial and to indicate localization judgments from the corner of their eyes. Either stationary bars (variable presentation time between 925 and 1,325 ms) or flashed bars (25 ms) were presented at a random position within the same rectangular space as that in the other localization trials. Thereafter, the modified FP vanished and a mouse pointer appeared at a random position 4° beyond the horizontal centerline of the screen. Subjects had to indicate the perceived position of the stationary or flashed bar without moving their eyes (cf. Fig. 1*B* for a timeline view). Thus, localization judgments were done on a completely dark stimulus screen without any visual references.

Sessions

Each subject participated in four experimental sessions, two with inward adaptation and two with outward adaptation. Experimental sessions were performed in random order. Before each experimental session subjects were informed about the particular task, the total number of trials, and the approximate duration of the session. Additionally, they were instructed to click in the outermost left corners of the stimulus screen whenever they were not able to localize the bar.

Course of an Experimental Session

Each session consisted of 180 preadaptation trials, 200 adaptation trials, and 180 postadaptation trials. Pre- and postadaptation phases contained all test localization trials, 15 each of target-on trials with a stationary bar, target-on trials with a flashed bar, target-off trials with a stationary bar, target-off trials with a flashed bar, fixation trials with a stationary bar, and fixation trials with a flashed bar. The remaining 90 trials in the pre- and postadaptation phases were reactive reinforcing trials without the target step in the prephase and with the 6° target step (inward/outward) in the postphase. All trials in the pre- and postadaptation phases were completely intermixed.

Data Analysis

Mathematica 7.0 was used for all data analysis. For a saccade to enter analysis, its starting point had to be within a circle of 2.5° diameter around the fixation point, 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. With these criteria 93.0 ± 2.0% (SE) of all trials with a saccade to perform were accepted in the inward adaptation experimental sessions and 92.5 ± 2.4% (SE) were accepted in the outward adaptation experimental sessions. In some trials during the pre- and postadaptation phases, subjects also had to localize a flashed or stationary bar after the saccade. Mouse clicks outside a circle of 8° diameter around the true bar position were excluded from analysis (<1%).

For fixation localization trials, gaze had to be within a circle of 2.5° diameter around the fixation point until the final mouse click. Within this circle, only microsaccades with an amplitude <1° were allowed; 95.9 ± 1.3% (SE) of all fixation localization trials were accepted in the inward adaptation experimental sessions and 96.5 ± 0.9% (SE) were accepted in the outward adaptation experimental sessions. Mouse clicks outside a circle of 8° diameter around the true bar position were excluded from analysis (<1%).

RESULTS

Adaptation

Figure 2 shows example sessions for inward (*A*) and outward (*B*) adaptation. Clearly there is a reduction of saccade amplitude during saccadic inward adaptation and an increase of saccade amplitude during saccadic outward adaptation for all trial types.

Averaged over all subjects the mean amplitude of pure reactive saccades before the adaptation phase was 18.78 ± 0.20° (SE) in the inward adaptation sessions and 18.55 ± 0.24° (SE) in the outward adaptation sessions (cf. horizontal gray rectangles in the prephase of Fig. 2, *A* and *B*). After inward adaptation the mean amplitude value of pure reactive saccades decreased to 14.36 ± 0.36° (SE) (cf. horizontal gray rectangle in the postphase of Fig. 2*A*). This decrease corresponded to a mean gain change of −23.6 ± 1.4% (SE). After outward

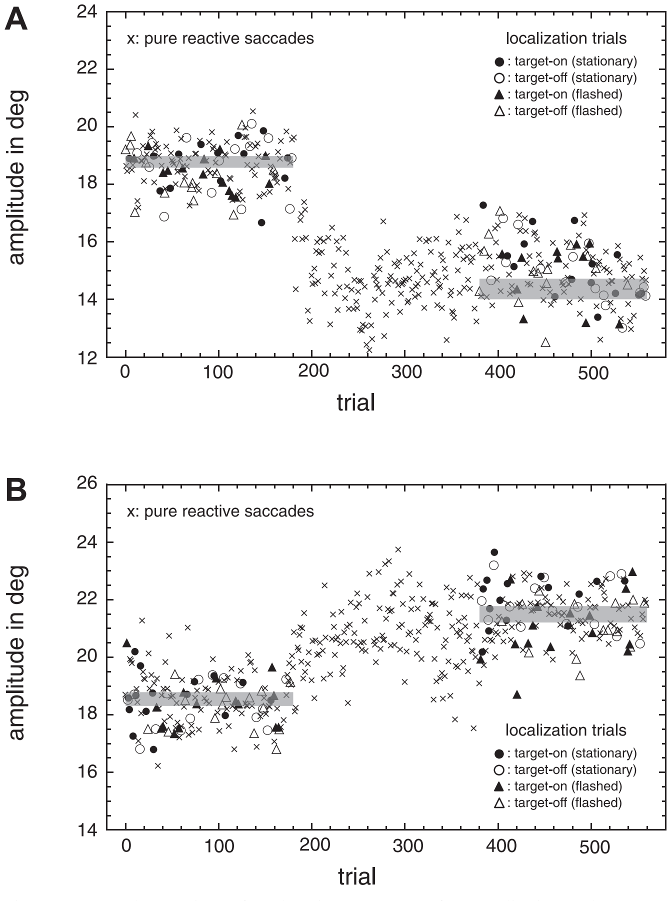

Fig. 2. Example sessions for the time course of saccadic inward (*A*) and outward (*B*) adaptation. The *crosses* indicate amplitude values in the preadaptation, adaptation, and postadaptation phases for trials without bar localization (pure reactive saccades). The *horizontal gray rectangles* give their means before and after adaptation. Their thickness indicates twice the SE. *Filled circles* indicate amplitude values in target-on localization trials with a stationary bar. *Open circles* indicate amplitude values in target-off localization trials with a stationary bar. *Filled triangles* indicate amplitude values in target-on localization trials with a flashed bar. *Open triangles* indicate amplitude values in target-off localization trials with a flashed bar.

adaptation the mean amplitude value of pure reactive saccades increased to 21.49 ± 0.28 (SE) (cf. horizontal gray rectangle in the postphase of Fig. 2*B*). This increase corresponded to a mean gain change of 15.9 ± 0.9% (SE). The gain change was significantly lower in the outward compared with the inward adaptation sessions (paired *t*-test with absolute values, $P < 0.0005$).

The gain change values for saccade trials with localization (circles and triangles) were similar to the gain change values for the pure reactive saccade trials. Thus, the presentation of the bar did not affect gain change [one-way repeated-measures ANOVA comparing gain change during pure reactive saccades, target-on localization trials (separate for stationary and flashed bars), and target-off localization trials (separate for stationary and flashed bars); inward: $F_{(4,48)} = 2.291$, $P = 0.073$; outward: $F_{(4,48)} = 1.905$, $P = 0.125$].

Localization After Reactive Saccades

Absolute mislocalization of stationary and flashed bars. To determine the mislocalization of stationary and flashed bars we compared localization judgments before and after adaptation in each condition. In each trial, the horizontal mouse click location relative to the horizontal true location of the bar was measured, and the resulting values were averaged to provide estimates of preadaptation and postadaptation localization judgments. Localization judgments of stationary bars before adaptation were −0.16 ± 0.17° (SE) [outward: −0.39 ± 0.18° (SE)] in the target-on condition and 0.02 ± 0.24° (SE) [outward: −0.48 ± 0.25° (SE)] in the target-off condition. For flashed bars localizations judgments before adaptation were −0.06 ± 0.23° (SE) [outward: −0.20 ± 0.29° (SE)] in the target-on condition and −0.26 ± 0.28° (SE) [outward: −0.61 ± 0.30° (SE)] in the target-off condition. After adaptation localizations judgments of stationary bars were −1.40 ± 0.42° (SE) [outward: 2.56 ± 0.25° (SE)] in the target-on condition and −0.98 ± 0.29° (SE) [outward: 1.87 ± 0.25° (SE)] in the target-off condition, and of flashed bars −3.23 ± 0.28° (SE) [outward: 3.30 ± 0.36° (SE)] in the target-on condition and −2.32 ± 0.24° (SE) [outward: 2.30 ± 0.29° (SE)] in the target-off condition. Negative values correspond to mislocalization against the original saccade direction; positive values indicate mislocalization in the original saccade direction.

To plot and statistically analyze the data we calculated the differences between preadaptation and postadaptation localization judgments for each condition. Figure 3 shows the mean adaptation-induced horizontal mislocalization [localization judgments (post) − localization judgments (pre)] of stationary and flashed bars in the target-on and target-off conditions after inward (*A*) and outward (*B*) adaptation. Negative values in *A* correspond to mislocalization against the original saccade direction (inward adaptation) and positive values in *B* indicate mislocalization in the original saccade direction (outward adaptation).

After inward adaptation and with a postsaccadic visual reference (target-on) the mean mislocalization of stationary bars was −1.24 ± 0.35° (SE) and the mean mislocalization of flashed bars was −3.17 ± 0.24° (SE). Both values were significantly different from zero (*t*-tests, stationary: $P < 0.005$; flashed: $P < 0.0005$). Without a postsaccadic visual reference (target-off) the mean mislocalization of stationary bars was −1.01 ± 0.26° (SE) and the mean mislocalization of flashed bars was −2.06 ± 0.19° (SE). Again both values were significantly different from zero (*t*-tests, stationary: $P < 0.005$; flashed: $P < 0.0005$).

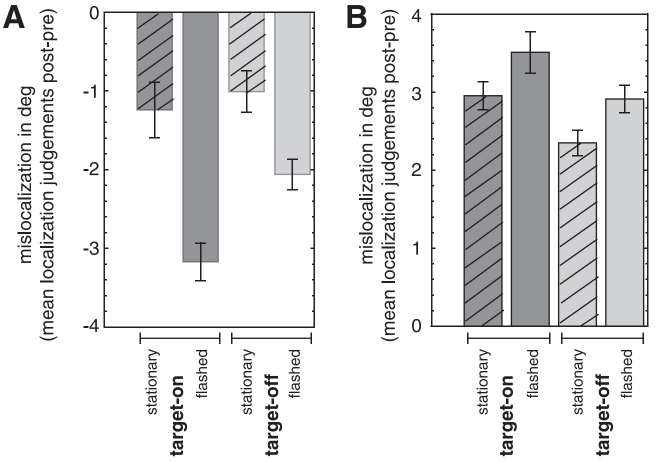

Fig. 3. Adaptation-induced mislocalization of stationary (*hatched bars*) and flashed stimuli (*solid bars*) after inward (*A*) and outward (*B*) adaptation of reactive saccades. *Dark gray bars* indicate mean adaptation-induced mislocalizations in the target-on conditions. *Light gray bars* indicate mean mislocalizations in the target-off conditions. Error bars are SE values.

After outward adaptation and with a postsaccadic visual reference (target-on) the mean mislocalization of stationary bars was 2.95 ± 0.18° (SE) and the mean mislocalization of flashed bars was 3.51 ± 0.27° (SE). Without a postsaccadic visual reference (target-off) the mean mislocalization of stationary bars was 2.35 ± 0.16° (SE) and the mean mislocalization of flashed bars was 2.91 ± 0.17° (SE). All values were significantly different from zero (*t*-tests, $P < 0.0005$).

A three-way repeated-measures ANOVA with factors adaptation direction (inward/outward), postsaccadic visual target reference (target-on/target-off), and bar type (stationary/flashed) showed a significant dependence of the mean mislocalization on all three main factors [adaptation direction: $F_{(1,12)} = 32.341$, $P < 0.0005$; postsaccadic visual target reference: $F_{(1,12)} = 30.348$, $P < 0.0005$; bar type: $F_{(1,12)} = 89.514$, $P < 0.0005$]. Additionally there was a significant interaction between adaptation direction and bar type [$F_{(1,12)} = 6.186$, $P < 0.05$] and between postsaccadic visual target reference and bar type [$F_{(1,12)} = 22.003$, $P < 0.005$]. The interaction of all three main factors was also significant [$F_{(1,12)} = 22.182$, $P < 0.005$].

Post hoc paired *t*-tests then revealed that after inward adaptation the mean mislocalization of flashed bars was significantly larger than the mean mislocalization of stationary bars (target-on, target-off, $P < 0.0005$). Comparison of the mean mislocalization in the target-on and target-off conditions revealed a contribution of the postsaccadic visual reference on final localization judgments. It was especially pronounced for the flashed bar condition, in which mean mislocalization in the target-on condition was significantly larger than the mean mislocalization in the target-off condition ($P < 0.0005$). For stationary bars the difference was not significant ($P = 0.11$), which might have to do with the smaller overall mislocalization. However, because in both cases mislocalization also occurred in the target-off conditions, postsaccadic target information cannot be the only source for the mislocalization; that is, the present target as a visual landmark can be responsible only for parts of the total mislocalization (cf., Awater and Lappe 2006; Deubel et al. 1996; McConkie and Currie 1996).

Furthermore, post hoc paired *t*-tests clarified that after saccadic outward adaptation, although not as pronounced as that after saccadic inward adaptation, mean mislocalizations of flashed bars (target-on/target-off) were significantly larger than mean mislocalizations of stationary bars (target-on/target-off) (target-on, target-off, $P < 0.005$). Consistent with a contribution of the postsaccadic visual reference on final localization judgments, mean mislocalizations in the target-on conditions (flashed/stationary) were significantly larger than mean mislocalizations in the target-off conditions (flashed/stationary) (flashed: $P < 0.005$; stationary: $P < 0.0005$).

Finally, the absolute values of mean mislocalizations of stationary bars (target-on/target-off) were significantly larger after saccadic outward adaptation than after saccadic inward adaptation (paired *t*-tests, target-on: $P < 0.0005$; target-off: $P < 0.0005$; note that in these tests values for inward adaptation were multiplied by -1 to make the two adaptation directions comparable). The difference was less pronounced in the mean mislocalizations of flashed bars in the target-off condition and not significant in the mean mislocalizations of flashed bars in the target-on condition [paired *t*-tests, target-on: $P = 0.08$; target-off: $P < 0.005$ (but close to 0.005)]. The larger difference in mean mislocalization of flashed bars between the target-on and target-off conditions after saccadic inward adaptation compared with after saccadic outward adaptation suggests a higher contribution of postsaccadic visual references to localization judgments after saccadic inward adaptation. The references provided by the saccade target induce mislocalization because the target stepped during the saccade. Thus, the reference information provided by the target is incorrect. Reliance on this information, therefore, contributes to mislocalization.

Comparison of mislocalization of stationary to flashed bars. We were interested in how much stationary bars were mislocalized in relation to flashed bars after inward and outward adaptation of reactive saccades. Therefore, we calculated the relative mislocalization (mislocalization of stationary bars divided by mislocalization of flashed bars) to normalize for the difference in mislocalization strength of flashed bars between the two adaptation directions.

Figure 4*A* shows the percentage ratio of mislocalization of stationary bars in relation to flashed bars after saccadic inward adaptation. The corresponding values are $37.9 \pm 9.3\%$ (SE) in the target-on condition and $49.8 \pm 12.1\%$ (SE) in the target-off condition. Figure 4*B* shows the ratio of mislocalization of stationary bars in relation to flashed bars after saccadic outward adaptation. The corresponding values are $86.3 \pm 4.6\%$ (SE) in the target-on condition and $82.6 \pm 5.8\%$ (SE) in the target-off condition. A two-way repeated-measures ANOVA with factors adaptation direction (inward/outward) and postsaccadic visual target reference (target-on/target-off) showed a significant dependence of the percentage amount of mislocalization on the adaptation direction [$F_{(1,12)} = 8.80$, $P < 0.05$]. The interaction was not significant [$F_{(1,12)} = 3.74$, $P = 0.08$]. Paired *t*-tests between the values after saccadic inward and outward adaptation confirmed that the ratio of mislocalization [(mean mislocalization of stationary bars/mean mislocalization of flashed bars) × 100] is significantly higher after outward adaptation than that after inward adaptation (target-on: $P < 0.005$; target-off: $P < 0.05$).

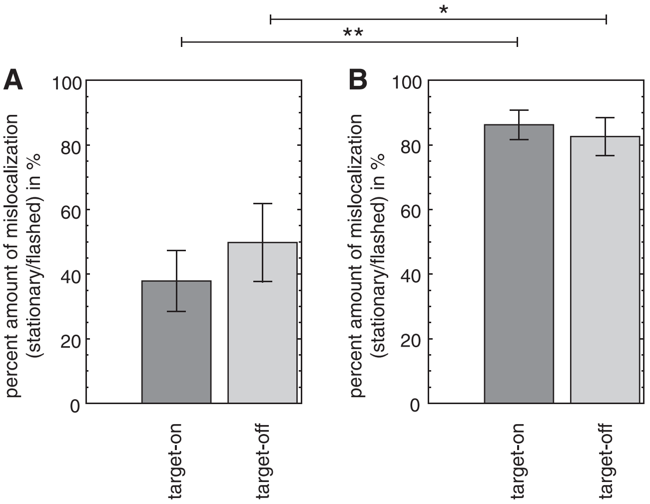

Fig. 4. Percentage ratio of adaptation-induced mislocalization of stationary bars in relation to flashed bars after inward (*A*) and outward (*B*) adaptation of reactive saccades (*dark gray*: target-on; *light gray*: target-off). Percentage ratio between the target-on conditions (inward: 37.9%; outward: 86.3%) as well as between the target-off conditions (inward: 49.8%; outward: 82.6%) were significantly different from each other [paired *t*-tests, $P < 0.005$ (target-on); $P < 0.05$ (target-off)]. Error bars are SE values.

Localization Judgments During Fixation

Localizations judgments during fixation and before adaptation were $-0.51 \pm 0.44^\circ$ (SE) [outward: $-0.86 \pm 0.48^\circ$ (SE)] for stationary bars and $-1.16 \pm 0.44^\circ$ (SE) [outward: $-1.54 \pm 0.46^\circ$ (SE)] for flashed bars. After adaptation localization judgments of stationary bars were $-0.71 \pm 0.38^\circ$ (SE) [outward: $0.57 \pm 0.52^\circ$ (SE)] and of flashed bars $-1.37 \pm 0.32^\circ$ (SE) [outward: $0.03 \pm 0.46^\circ$ (SE)].

Figure 5 shows the mean adaptation-induced mislocalizations [localization judgments (post) − localization judgments (pre)] of stationary and flashed bars during fixation.

There was no significant mislocalization after inward adaptation (*t*-tests, stationary: $P = 0.20$; flashed: $P = 0.20$). After outward adaptation, however, both flashed and stationary bars were significantly mislocalized, with quite similar magnitude [stationary: $1.43 \pm 0.22^\circ$ (SE); flashed: $1.57 \pm 0.21^\circ$ (SE), *t*-tests, $P < 0.0005$]. A two-way repeated-measures ANOVA with factors adaptation direction (inward/outward) and bar type (stationary/flashed) corroborate the similar magnitude of mislocalizations of both bar types [$F_{(1,12)} = 0.24$, $P = 0.63$, interaction: $F_{(1,12)} = 0.30$, $P = 0.59$] and the significantly larger mislocalizations after outward than after inward adaptation of reactive saccades [$F_{(1,12)} = 23.23$, $P < 0.0005$].

DISCUSSION

Our results showed that the ratio of mislocalization of stationary bars in relation to flashed bars was higher after saccadic outward adaptation than that after saccadic inward adaptation of reactive saccades. During periods of fixation neither bar type was mislocalized after saccadic inward adaptation but both were mislocalized after outward adaptation.

Our study was conducted to corroborate the differences between saccadic inward and outward adaptation, observed in

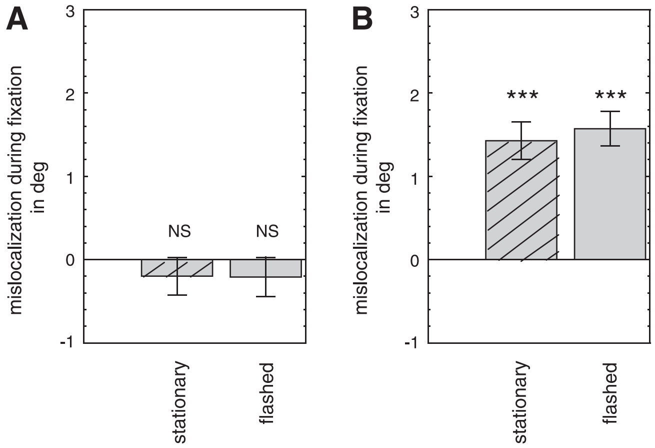

Fig. 5. Mean mislocalization of stationary (*hatched*) and flashed (*solid*) bars after inward (*A*) and outward (*B*) adaptation of reactive saccades during fixation. No significant mean mislocalizations were observed for stationary and flashed bars after saccadic inward adaptation (NS, $P > 0.05$ in both *t*-tests). Both bar types were significantly mislocalized after saccadic outward adaptation (***$P < 0.0005$ in both *t*-tests). Error bars are SE values.

the study of Schnier and Lappe (2011), by establishing the link between these results and those of Zimmermann and Lappe (2009) who investigated changes in visual localization for two different probe durations [i.e., a long-duration (stationary) probe and a short-duration (flashed) probe], after inward adaptation of reactive and scanning saccades. They found that flashed but not stationary probes were mislocalized after inward adaptation of reactive saccades. However, both probes were mislocalized after inward adaptation of scanning saccades. Since there is strong transfer of inward adaptation from scanning to reactive saccades, but only weak transfer in the opposite direction (Alahyane et al. 2007; Collins and Doré-Mazars 2006; Cotti et al. 2007; Deubel 1999; Pélisson et al. 2010) and, since stationary localization probes resemble typical targets for scanning while flashed probes resemble targets for reactive saccades, the asymmetry of mislocalization suggests that the selectivity of visual mislocalization after inward adaptation of a particular saccade type fits the adaptation selectivity in the motor behavior (Zimmermann and Lappe 2009).

Schnier and Lappe (2011) studied adaptation transfer after outward adaptation. Transfer from reactive to scanning and overlap saccades was stronger after outward than after inward adaptation. In the light of the above considerations, this predicted that stationary localization probes should be more mislocalized after outward than after inward adaptation of reactive saccades. Indeed, when we compared the relative amount of mislocalization of stationary versus flashed bars after saccadic inward adaptation with the corresponding values after saccadic outward adaptation (cf. Fig. 4) this is exactly what we found. Also as expected, the absolute mislocalization of stationary bars was higher after outward adaptation than that after inward adaptation (cf. Fig. 3). Since this was also true for flashed bars, effects of saccadic outward adaptation on visual localization and effects of saccadic inward adaptation on visual localization must rely on different processes. One might speculate that an essential difference lies in the substantial visual error that persists after saccadic outward adaptation but not after saccadic inward adaptation, since outward adaptation remains incomplete for much longer than inward adaptation (Zimmermann and Lappe 2010). Indeed, when inducing adaptation with a long-lasting postsaccadic visual error (Robinson et al. 2003) Zimmermann and Lappe (2010) revealed mislocalization during fixation also after the inward adaptation procedure. In addition, the availability of postsaccadic target information also provided a contribution to the mislocalization, as seen by a larger amount of mislocalization in the target-on conditions compared with the target-off conditions for both inward and outward adaptation. Thus, the postsaccadic target is used as a visual landmark, but is responsible only for parts of the mislocalization (Awater and Lappe 2006; Deubel et al. 2002; McConkie and Currie 1996).

Now one might ask at which neural stage outward adaptation of reactive saccades differs from inward adaptation of reactive saccades, and how this difference leads to the observed differences in mislocalization of stationary versus flashed localization probes. It is unlikely that the difference lies close to the motor stage (i.e., late in oculomotor processing) because then it should not affect perception differently. Rather outward adaptation of reactive saccades appears to differ from inward adaptation at the target registration or saccade planning stages (Cotti et al. 2007, 2009; Ethier et al. 2008; Hernandez et al. 2008; Panouilleres et al. 2009; Zimmermann and Lappe 2010). Consequently, this means that the differences in localization judgments of stationary probes in relation to flashed probes between inward and outward adaptation should be based on early target localization or planning stages, which are used in the localization judgments of stationary bars, which are more strongly modulated after outward adaptation than after inward adaptation of reactive saccades. This suggestion is consistent with the observations of a higher amount of transfer from reactive saccades to long-duration overlap and scanning saccades after outward adaptation than after inward adaptation (Schnier and Lappe 2011) if the use of target registration or planning stages depends on the presentation duration of the localization probe or the saccade target (Schnier and Lappe 2011). This in turn would be consistent with the results of Cotti et al. (2007, 2009), which suggest that target registration or planning stages are modulated after saccadic inward adaptation of voluntarily triggered scanning saccades.

Figure 5 shows that even during fixation, flashed and stationary bars were mislocalized after the participant underwent saccadic outward adaptation. This finding replicates the results that Zimmermann and Lappe (2010) obtained with flashed stimuli and extends them to stimuli that are continuously visible. The mislocalization during fixation may be explained if localization judgments during fixation use target registration or planning stages that are modulated after saccadic outward but not after saccadic inward adaptation. The similarity of stationary and flashed data might suggest that the use of target registration stages in localization judgments during fixation is independent of the localization probe duration.

On a neuronal level, target localization may involve neurons with long integration times that might respond to stationary as well as flashed bars. Thus, whenever those neurons are affected by adaptation of a particular saccade type or in a particular direction mislocalization of both probe types should occur. We suggest that this is the case for outward adaptation of reactive saccades, but would assume a similar localization behavior for scanning saccades, independent of the direction of target displacement.

The localization targets in our study were located close to the adapted saccade target. Several previous studies have shown that adaptation-induced mislocalization depends on the location of the probe. Awater et al. (2005), Collins et al. (2007), and Schnier et al. (2010) have presented detailed investigations of the spatial range of mislocalization. Since these studies were mostly concerned with localization after adapted saccades, it would also be interesting to investigate in detail the spatial specificity of the mislocalization effect during fixation described in the present study.

In summary, our results show that outward adaptation of reactive saccades and of scanning saccades have an important influence on localization judgments in common, that is, the high amount of mislocalization of stationary bars (cf. Zimmermann and Lappe 2009). This common mislocalization is likely to stem from early target registration stages that are modulated after outward adaptation of reactive saccades as well as after adaptation of scanning saccades. Consistent with this hypothesis we revealed mislocalization of stationary and flashed bars even during fixation. Accordingly, we suggest that stationary and flashed bars should also be mislocalized after adaptation of scanning saccades and during fixation to support the common modulated target registration or planning stage of the outward adaptation procedure of reactive saccades and the adaptation procedure of scanning saccades. Two aspects directly lead to this assumption. First, the adaptation transfer from reactive to overlap or scanning saccades is higher after outward than that after inward adaptation of reactive saccades, suggesting a common adaptation locus between outward adaptation of reactive saccades and scanning saccades, probably before the sensory-motor transformations (Schnier and Lappe 2011). Second, adaptation of voluntary (scanning) saccades transfers to hand-pointing movements (Cotti et al. 2007) or to antisaccades in the nonadapted direction (Cotti et al. 2009), suggesting a deep involvement of target registration or planning stages in the scanning adaptation procedure.

GRANTS

This work was supported by German Science Foundation Grants DFGLA-952/3 and DFG LA-952/4 (M.L.), 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 authors.

AUTHOR CONTRIBUTIONS

F.S. and M.L. conception and design of research; F.S. performed experiments; F.S. and M.L. analyzed data; F.S. and M.L. interpreted results of experiments; F.S. prepared figures; F.S. and M.L. drafted manuscript; F.S. and M.L. edited and revised manuscript; F.S. and M.L. approved final version of manuscript.

REFERENCES

Abel LA, Schmidt D, Dell'Osso LF, Daroff RB. Saccadic system plasticity in humans. *Ann Neurol* 4: 313–318, 1978.

Alahyane N, Salemme R, Urquizar C, Cotti J, Guillaume A, Vercher JL, Pélisson D. Oculomotor plasticity: are mechanisms of adaptation for reactive and voluntary saccades separate? *Brain Res* 1135: 107–121, 2007.

Albano JE, King WM. Rapid adaptation of saccadic amplitude in humans and monkeys. *Invest Ophthalmol Vis Sci* 30: 1883–1893, 1989.

Awater H, Burr D, Lappe M, Morrone MC, Goldberg ME. Effects of saccadic adaptation on localization of visual targets. *J Neurophysiol* 93: 3605–3614, 2005.

Awater H, Lappe M. Mislocalization of perceived saccade target position induced by perisaccadic visual stimulation. *J Neurosci* 26: 12–20, 2006.

Bahcall DO, Kowler E. Illusory shifts in visual direction accompany adaptation of saccadic eye movements. *Nature* 400: 864–866, 1999.

Bruno A, Morrone MC. Influence of saccadic adaptation on spatial localization: comparison of verbal and pointing reports. *J Vis* 7: 1–12, 2007.

Cecala AL, Freedman EG. Amplitude changes in response to target displacements during human eye-head movements. *Vision Res* 48: 149–166, 2008.

Cecala AL, Freedman EG. Head-unrestrained gaze adaptation in the rhesus macaque. *J Neurophysiol* 101: 164–183, 2009.

Collins T, Dore-Mazars K. Eye movement signals influence perception: evidence from the adaptation of reactive and volitional saccades. *Vision Res* 46: 3659–3673, 2006.

Collins T, Dore-Mazars K, Lappe M. Motor space structures perceptual space: evidence from human saccadic adaptation. *Brain Res* 1172: 32–39, 2007.

Collins T, Rolfs M, Deubel H, Cavanagh P. Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *J Vis* 9: 29.1–29.9, 2009.

Cotti J, Guillaume A, Alahyane N, Pélisson D, Vercher JL. Adaptation of voluntary saccades, but not of reactive saccades, transfers to hand pointing movements. *J Neurophysiol* 98: 602–612, 2007.

Cotti J, Panouilleres M, Munoz DP, Vercher JL, Pélisson D, Guillaume A. Adaptation of reactive and voluntary saccades: different patterns of adaptation revealed in the antisaccade task. *J Physiol* 587: 127–138, 2009.

Deubel H. Adaptivity of gain and direction in oblique saccades. In: *Eye Movements: From Physiology to Cognition*, edited by O'Regan JK, Levy-Schoen A. New York: Elsevier/North-Holland, 1987, p. 181–190.

Deubel H. Separate adaptive mechanisms for the control of reactive and volitional saccadic eye movements. *Vision Res* 35: 3529–3540, 1995.

Deubel H. Separate mechanisms for the adaptive control of reactive, volitional and memory guided saccadic eye movements. In: *Attention and Performance XVII: Cognitive Regulation of Performance*, edited by Gopher D, Koriat A. Cambridge, MA: MIT Press, 1999, p. 697–721.

Deubel H, Schneider WX, Bridgeman B. Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Res* 36: 985–996, 1996.

Deubel H, Schneider WX, Bridgeman B. Transsaccadic memory of position and form. In: *The Brain's Eye: Neurobiological and Clinical Aspects of Oculomotor Research*, edited by Hyona WHJ, Munoz DP, Radach R. Amsterdam, The Netherlands: Elsevier, 2002, p. 165–180.

Deubel H, Wolf W, Hauske G. Adaptive gain control of saccadic eye movements. *Hum Neurobiol* 5: 245–253, 1986.

Erkelens CJ, Hulleman J. Selective adaptation of internally triggered saccades made to visual targets. *Exp Brain Res* 93: 157–164, 1993.

Ethier V, Zee DS, Shadmehr R. Changes in control of saccades during gain adaptation. *J Neurosci* 28: 13929–13937, 2008.

Frens MA, Van Opstal AJ. Transfer of short-term adaptation in human saccadic eye movements. *Exp Brain Res* 100: 293–306, 1994.

Fujita M, Amagai A, Minakawa F, Aoki M. Selective and delay adaptation of human saccades. *Brain Res Cogn Brain Res* 13: 41–52, 2002.

Garaas TW, Pomplun M. Distorted object perception following whole-field adaptation of saccadic eye movements. *J Vis* 11: 1–11, 2011.

Gaveau V, Alahyane N, Salemme R, Desmurget M. Self-generated saccades do not modify the gain of adapted reactive saccades. *Exp Brain Res* 162: 526–531, 2005.

Gaymard B, Lynch J, Ploner CJ, Condy C, Rivaud-Pechoux S. The parieto-collicular pathway: anatomical location and contribution to saccade generation. *Eur J Neurosci* 17: 1518–1526, 2003.

Georg K, Hamker FH, Lappe M. Influence of adaptation state and stimulus luminance on peri-saccadic localization. *J Vis* 8: 15.1–15.11, 2008.

Georg K, Lappe M. Effects of saccadic adaptation on visual localization before and during saccades. *Exp Brain Res* 129: 9–23, 2009.

Golla H, Tzidris K, Haarmeier T, Catz N, Barash S, Thier P. Reduced saccadic resilience and impaired saccadic adaptation due to cerebellar disease. *Eur J Neurosci* 27: 132–144, 2008.

Havermann K, Lappe M. The influence of the consistency of postsaccadic visual errors on saccadic adaptation. *J Neurophysiol* 103: 3302–3310, 2010.

Havermann K, Zimmermann E, Lappe M. Eye position effects in saccadic adaptation. *J Neurophysiol* 106: 2536–2545, 2011.

Hernandez TD, Levitan CA, Banks MS, Schor CM. How does saccade adaptation affect visual perception? *J Vis* 8: 1–16, 2008.

Hopp JJ, Fuchs AF. The characteristics and neuronal substrate of saccadic eye movement plasticity. *Prog Neurobiol* 72: 27–53, 2004.

Kommerell G, Olivier D, Theopold H. Adaptive programming of phasic and tonic components in saccadic eye movements. Investigations of patients with abducens palsy. *Invest Ophthalmol Vis Sci* 15: 657–660, 1976.

Kroller J, Pélisson D, Prablanc C. On the short-term adaptation of eye saccades and its transfer to head movements. *Exp Brain Res* 111: 477–482, 1996.

McConkie GW, Currie CB. Visual stability across saccades while viewing complex pictures. *J Exp Psychol Hum Percept Perform* 22: 563–581, 1996.

McLaughlin SC. Parametric adjustment in saccadic eye movements. *Percept Psychophys* 2: 359–362, 1967.

McLaughlin SC, Kelly M, Anderson R, Wenz T. Localization of a peripheral target during parametric adaptation of saccadic eye movements. *Percept Psychophys* 4: 45–48, 1968.

Miller JM, Anstis T, Templeton WB. Saccadic plasticity: parametric adaptive control by retinal feedback. *J Exp Psychol Hum Percept Perform* 7: 356–366, 1981.

Moidell BG, Bedell HE. Changes in oculocentric visual direction induced by the recalibration of saccades. *Vision Res* 28: 329–336, 1988.

Müri RM, Nyffeler T. A hundred years of eye movement research in psychiatry: neurophysiology and neuroanatomy of reflexive and volitional saccades as revealed by lesion studies with neurological patients and transcranial magnetic stimulation (TMS). *Brain Cogn* 68: 284–292, 2008.

Noto CT, Robinson FR. Visual error is the stimulus for saccade gain adaptation. *Brain Res Cogn Brain Res* 12: 301–305, 2001.

Optican LM, Zee DS, Chu FC. Adaptive response to ocular muscle weakness in human pursuit and saccadic eye movements. *J Neurophysiol* 54: 110–122, 1985.

Panouilleres M, Urquizar C, Salemme R, Pélisson D. Sensory processing of motor inaccuracy depends on previously performed movement and on subsequent motor corrections: a study of the saccadic system. *PLoS One* 6: e17329, 2011.

Panouilleres M, Weiss T, Urquizar C, Salemme R, Munoz DP, Pélisson D. Behavioural evidence of separate adaptation mechanisms controlling saccade amplitude lengthening and shortening. *J Neurophysiol* 101: 1550–1559, 2009.

Pierrot-Deseilligny C. Cortical control of saccades. *Neuroophthalmology* 11: 63–75, 1991.

Pélisson D, Alahyane N, Panouilleres M, Tilikete C. Sensorimotor adaptation of saccadic eye movements. *Neurosci Biobehav Rev* 34: 1103–1120, 2010.

Rivaud S, Müri RM, Gaymard B, Vermersch AI, Pierrot-Deseilligny C. Eye movement disorders after frontal eye field lesions in humans. *Exp Brain Res* 102: 110–120, 1994.

Robinson FR, Noto CT, Bevans SE. Effect of visual error size on saccade adaptation in monkey. *J Neurosci* 90: 1235–1244, 2003.

Schnier F, Lappe M. Differences in intersaccadic adaptation transfer between inward and outward adaptation. *J Neurophysiol* 106: 1399–1410, 2011.

Schnier F, Zimmermann E, Lappe M. Adaptation and mislocalization fields for saccadic outward adaptation in humans. *J Eye Mov Res* 3: 1–18, 2010.

Semmlow JL, Gauthier GM, Vercher JL. Mechanisms of short-term saccadic adaptation. *J Exp Psychol Hum Percept Perform* 15: 249–258, 1989.

Shafer JL, Noto CT, Fuchs AF. Temporal characteristics of error signals driving saccadic gain adaptation in the macaque monkey. *J Neurophysiol* 84: 88–95, 2000.

Straube A, Deubel H. Rapid gain adaptation affects the dynamics of saccadic eye movements in humans. *Vision Res* 35: 3451–3458, 1995.

Straube A, Fuchs AF, Usher S, Robinson FR. Characteristics of saccadic gain adaptation in rhesus macaques. *J Neurophysiol* 77: 874–895, 1997.

Wallman J, Fuchs AF. Saccadic gain modification: visual error drives motor adaptation. *J Neurophysiol* 80: 2405–2416, 1998.

Zimmermann E, Lappe M. Mislocalization of flashed and stationary visual stimuli after adaptation of reactive and scanning saccades. *J Neurosci* 29: 11055–11064, 2009.

Zimmermann E, Lappe M. Motor signals in visual localization. *J Vis* 10: 2.1–2.11, 2010.

Zimmermann E, Lappe M. Eye position effects in oculomotor plasticity and visual localization. *J Neurosci* 31: 7341–7348, 2011.