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

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Abstract

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 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 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 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.

Keywords

Saccade, adaptation, eye movements, visual localization, stationary bars, flashed bars

Introduction

Clear vision is based on the ability to make saccades as accurately as possible. The accuracy of the saccadic system is maintained by the mechanism of saccadic adaptation. Saccadic inaccuracies may occur as a consequence of eye muscle weakness (Kommerell et al., 1976; Abel et al., 1978; Optican et al., 1985) but may also be artificially generated and studied in the laboratory by a systematic intra-saccadic displacement of the saccade target (McLaughlin, 1967; Miller et al., 1981). The resulting difference between the eye landing position and the post-saccadic visual location of the target induces the adjustment of transformation parameters between the visual input and the motor commands. This adjustment reduces the post-saccadic 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 post-saccadic error (Wallman & Fuchs, 1998; Shafer et al., 2000; Noto & Robinson, 2001; Collins et al., 2009; Havermann & Lappe, 2010; Zimmermann & Lappe, 2010; Panouilleres et al., 2011).

Saccadic adaptation is specific to the direction and amplitude of the saccade (Deubel et al., 1986; Deubel, 1987; Albano & King, 1989; Frens & Van Opstal, 1994; Collins et al., 2007; Schnier et al., 2010), to the initial eye position (Zimmermann & Lappe, 2011; Havermann et al., 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 & Fuchs, 2004). Because there is only limited time to integrate spatio-temporal target information reactive saccades are thought to receive target localization signals from comparatively early visual areas in the oculomotor pathway (Pierrot-Deseilligny, 1991; Gaymard et al., 2003; Müri & Nyffeler, 2008). 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 & Fuchs, 2004). Because there is more time to integrate spatio-temporal target information overlap saccades might receive target localization signals from higher visual areas in the oculomotor pathway (Deubel, 1999; Rivaud et al., 1994; Müri & Nyffeler, 2008). 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 & 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

(Erkelens & Hulleman, 1993; Fujita et al., 2002; Gaveau et al., 2005; Collins & Doré-Mazars, 2006; Cotti et al., 2007; Zimmermann & Lappe, 2009). Because of the non-zero 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 than 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 & 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 & Morrone, 2007; Collins et al., 2007; Georg & Lappe, 2009; Schnier et al., 2010), the pointing to a flashed target with the hand (Cotti et al., 2007; Bruno & Morrone, 2007; Hernandez et al., 2008; Cotti et al., 2009; but see Kroller et al., 1996, McLaughlin et al., 1968, Cecala and Freedman, 2008, 2009), and even the apparent position of the saccade target itself (Bahcall & Kowler, 1999). The strength of mislocalization depends on the saccade type, but also on the properties of the target. Zimmermann & 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 while stationary localization probes were only mislocalized 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 (Deubel, 1999; Collins & Doré-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2007; 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 judgements and saccade targeting share a common representation. This is also supported by findings that mislocalization also occurs during periods of fixation (Moidell and Bedell, 1988, Zimmermann and Lappe, 2010, Schnier et al., 2010, Garaas and Pomplun, 2011), suggesting that saccadic adaptation affects visual localization at the target registration or planning stages.
There is a second factor that divides saccadic adaptation properties, namely 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 (Miller et al., 1981; Semmlow et al., 1989; Straube & Deubel, 1995; Straube et al., 1997; Hernandez et al., 2008; Golla et al., 2008; Ethier et al., 2008; Panouilleres et al., 2009; Zimmermann & Lappe, 2010; Schnier & Lappe, 2011). Finally, differences have been also observed in the adjustment of saccade dynamics (peak velocity, duration) between the inward and outward adaptation procedures (Golla et al. 2008; Ethier et al. 2008; Schnier and Lappe, 2010).

Transfer from reactive saccades to overlap and scanning saccades is significantly stronger after outward adaptation than after inward adaptation (Schnier & 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 & 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 & Lappe (2011) and Ethier et al. (2008) suggest that there is a stronger modulation of target localization stages after outward than 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 or not. 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 spatio-temporal 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 & 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 judgements 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; Cotti et al., 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" monitor (Eizo FlexScan F930) with a vertical frequency of 120 Hz at a resolution of 1024 x 768 pixels. Participants were seated 57 cm in front of the stimulus monitor with their chin supported by a chin rest. This setting results in a visual field of 40 deg x 30 deg. Experiments were done in complete darkness with a background luminance below 0.0006 cd/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 (cf. Georg et al. (2008) for a detailed description).

Eye movement recording

Eye movements were recorded with an EyeLink 1000 eye tracker (Desktop Mount Base System, SR Research, LTD, Canada) using signals from the pupil and the corneal reflex. The recorded data comprised online events and raw gaze position samples (at 1000 Hz) from the tracked left eye. Saccades were detected online as soon as eye velocity crossed a velocity threshold of 22 deg/sec and an acceleration threshold of 4000 deg/sec^2. Messages were written into the eyelink file in order 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 deg 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 deg 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 towards the simultaneously appearing target T1, which was 8 deg to the right of the center of the screen inducing a 20 deg reactive saccade. When eye position exceeded a three deg trigger threshold rightwards from FP (saccade onset), the target T1 stepped 6 deg inwards, or 6 deg outwards 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 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 deg to the left of the center of the screen. Correct fixation was the trigger to proceed with the trial.

Localization judgements of stationary bars

A bar (width 0.3 deg, height 2 deg, and luminance 0.13 cd/m^2) was presented at a random position within a rectangular space (width 4 deg, height 2 deg) centered 2 deg directly above the target position T1. After a variable time between 800 and 1200 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 further 500 ms. Thereafter a mouse pointer appeared at a random position 4

deg beyond the horizontal centerline of the screen and subjects had to indicate the perceived position of the stationary bar (cf. Figure 1 A for a timeline view). Thus, localization judgements 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 post-saccadic visual references that might affect the localization judgement. Accordingly, the trials in which the target remained visible after the saccade were named target-on trials.

Localization judgements of flashed bars

The FP remained visible for a variable time between 800 and 1200 ms. Then, the fixation point was extinguished, the target T1 appeared, and subjects performed a saccade to T1. 80 ms after T1 appearance 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 deg, height 2 deg) centered 2 deg directly above the target position T1. After saccade onset the target disappeared during target-off trials, or remained visible for further 500 ms during target-on trials. Thereafter a mouse pointer appeared at a random position 4 deg beyond the horizontal centerline of the screen. Subjects had to indicate the perceived position of the flashed bar (cf. Figure 1 A for a timeline view). Thus, localization judgements 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 1200 ms together with FP whereas in the latter the bar was flashed for 25 ms after FP was turned off.

Figure 1 about here

Localization judgements 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 deg and a thickness of 0.1 deg, reminded subjects to keep fixation during the following trial and to indicate localization judgements from the corner of their eyes. Either stationary bars (variable presentation time between 925 ms - 1325 ms) or flashed bars (25 ms) were presented at a random position within the same rectangular space as in the other localization trials. Thereafter the modified FP vanished and a mouse pointer appeared at a random position 4 deg 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. Figure 1 B for a timeline view). Thus, localization judgements 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 pre-adaptation trials, 200 adaptation trials, and 180 post-adaptation trials. Pre- and post-adaptation 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 post-adaptation phases were reactive reinforcing trials without the target step in the pre-phase and with the 6 deg target step (inward/outward) in the post-phase. All trials in the pre- and post-adaptation phases were completely intermixed.

Data analysis

Mathematica 7.0 was used for all data analysis. For a saccade to enter analysis, its start point had to be within a circle of 2.5 deg diameter around the fixation point, its amplitude had to be between 10 and 30 deg, its duration had to be between 20 and 100 ms, and its latency had to be between 80 and 400 ms. 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 post-adaptation phase, subjects also had to localize a flashed or stationary bar after the saccade. Mouse clicks outside a circle of 8 deg diameter around the true bar position were excluded from analysis (less than 1%).

For fixation localization trials, gaze had to be within a circle of 2.5 deg diameter around the fixation point

until the final mouse click. Within this circle only microsaccades with an amplitude less than 1 deg 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 deg diameter around the true bar position were excluded from analysis (less than 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 adaptation phase was 18.78 deg ± 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 pre-phase of figures 2 A and B). After inward adaptation the mean amplitude value of pure reactive saccades decreased to 14.36 deg ± 0.36 (SE) (cf. horizontal gray rectangle in the post-phase of figure 2 A). This decrease corresponded to a mean gain change of -23.6 % ± 1.4 (SE). After outward adaptation the mean amplitude value of pure reactive saccades increased to 21.49 ± 0.28 (SE) (cf. horizontal gray rectangle in the post- phase of figure 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 to 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 (oneway 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: $F(4,48)=1.905$, $p=0.125$).

Figure 2 about here

Localization after reactive saccades

Absolute mislocalization of stationary and flashed bars

To determine the mislocalization of stationary and flashed bars we compared localization judgements 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 pre-adaptation and post-adaptation localization judgements. Localization judgements of stationary bars before adaptation were -0.16 deg ± 0.17 (SE) (outward: -0.39 deg ± 0.18 (SE)) in the target-on condition and 0.02 deg ± 0.24 (SE) (outward: -0.48 deg ± 0.25 (SE)) in the target-off condition. For flashed bars localizations judgements before adaptation were -0.06 deg ± 0.23 (SE) (outward: -0.20 deg ± 0.29 (SE)) in the target-on condition and -0.26 deg ± 0.28 (SE) (outward: -0.61 deg ± 0.30 (SE)) in the target-off condition. After adaptation localizations judgements of stationary bars were -1.40 deg ± 0.42 (SE) (outward: 2.56 deg ± 0.25 (SE)) in the target-on condition and -0.98 deg ± 0.29 (SE) (outward: 1.87 deg ± 0.25 (SE)) in the target-off condition, and of flashed bars -3.23 deg ± 0.28 (SE) (outward: 3.30 deg ± 0.36 (SE)) in the target-on condition and -2.32 deg ± 0.24 (SE) (outward: 2.30 deg ± 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 pre-adaptation and post-adaptation localization judgements for each condition. Figure 3 shows the mean adaptation-induced horizontal mislocalization (localization judgements (post) – localization judgements (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), positive values in B indicate mislocalization in the original saccade direction (outward adaptation).

Figure 3 about here

After inward adaptation and with a post-saccadic visual reference (target-on) the mean mislocalization of stationary bars was -1.24 deg ± 0.35 (SE) and the mean mislocalization of flashed bars was -3.17 deg ± 0.24 (SE). Both values were significantly different from zero (t-tests, stationary: $p<0.005$, flashed: $p<0.0005$). Without a post-saccadic visual reference (target-off) the mean mislocalization of stationary bars was -1.01 deg ± 0.26 (SE) and the mean mislocalization of flashed bars was -2.06 deg ± 0.19 (SE). Again both values were significantly different from zero (t-tests, stationary: $p<0.005$, flashed: $p<0.0005$). After outward adaptation and with a post-saccadic visual reference (target-on) the mean mislocalization of stationary bars was 2.95 deg ± 0.18 (SE) and the mean mislocalization of flashed bars was 3.51 deg ±

0.27 (SE). Without a post-saccadic visual reference (target-off) the mean mislocalization of stationary bars was 2.35 deg ± 0.16 (SE) and the mean mislocalization of flashed bars was 2.91 deg ± 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), post-saccadic 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: $F(1,12)=32.341$, $p<0.0005$; post-saccadic 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 post-saccadic visual target reference and bar type ($F(1,12)=22.003$, $p<0.005$). The interaction of all three main factors was also signifcant ($F(1,12)=22.182$, $p<0.005$).

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 post-saccadic visual reference on final localization judgements. It was especially pronounced for the flashed bar condition, in which mean mislocalization in the target-on condition was significantly larger than 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 occurred also in the target-off conditions, post-saccadic target information cannot be the only source for the mislocalization, i.e. the present target as a visual landmark can be only responsible for parts of the total mislocalization (cf. McConkie & Currie (1996); Deubel et al. (1996); Awater & Lappe (2006)).

Furthermore, post-hoc paired t-tests clarified that after saccadic outward adaptation, although not as pronounced as 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 post-saccadic visual reference on final localization judgements, 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) in order 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

399 the mean mislocalizations of flashed bars in the target-on condition (paired t-tests, target-on: $p=0.08$, tar-
400 get-off: $p<0.005$ (but close to 0.005)). The larger difference in mean mislocalization of flashed bars be-
401 tween the target-on and target-off conditions after saccadic inward adaptation in comparison to after sac-
402 cadic outward adaptation suggest a higher contribution of post-saccadic visual references to localization
403 judgements after saccadic inward adaptation. The references provided by the saccade target induce mis-
404 localization because the target stepped during the saccade. Thus, the reference information provided by
405 the target is incorrect. Reliance on this information, therefore, contributes to mislocalization.
406
407 **Comparison of mislocalization of stationary to flashed bars**
408
409 We were interested in how much stationary bars were mislocalized in relation to flashed bars after in-
410 ward and outward adaptation of reactive saccades. Therefore, we calculated the relative mislocalization
411 (mislocalization of stationary bars divided by mislocalization of flashed bars) to normalize for the differ-
412 ence in mislocalization strength of flashed bars between the two adaptation directions.
413
414 Figure 4 about here
415
416 Figure 4 A shows the percentage ratio of mislocalization of stationary bars in relation to flashed bars af-
417 ter saccadic inward adaptation. The corresponding values are 37.9 % ± 9.3 (SE) in the target-on condi-
418 tion and 49.8 % ± 12.1 (SE) in the target-off condition. Figure 4 B shows the ratio of mislocalization of
419 stationary bars in relation to flashed bars after saccadic outward adaptation. The corresponding values are
420 86.3 % ± 4.6 (SE) in the target-on condition and 82.6 % ± 5.8 (SE) in the target-off condition. A two-
421 way repeated measures ANOVA with factors adaptation direction (inward/outward) and post-saccadic
422 visual target reference (target-on/target-off) showed a significant dependence of the percent amount of
423 mislocalization on the adaptation direction ($F(1,12)=8.80$, $p<0.05$). The interaction was not significant
424 ($F(1,12)=3.74$, $p=0.08$). Paired t-tests between the values after saccadic inward and outward adaptation
425 confirmed that the ratio of mislocalization (mean mislocalization of stationary bars/mean mislocalization
426 of flashed bars • 100) is significantly higher after outward adaptation than after inward adaptation (tar-
427 get-on: $p<0.005$, target-off: $p<0.05$).
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431 **Localization judgements during fixation**
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Localizations judgements during fixation and before adaptation were -0.51 deg ± 0.44 (SE) (outward: -0.86 deg ± 0.48 (SE)) for stationary bars and -1.16 deg ± 0.44 (SE) (outward: -1.54 deg ± 0.46 (SE)) for flashed bars. After adaptation localization judgements of stationary bars were -0.71 deg ± 0.38 (SE) (outward: 0.57 deg ± 0.52 (SE)) and of flashed bars -1.37 deg ± 0.32 (SE) (outward: 0.03 deg ± 0.46 (SE)).

Figure 5 shows the mean adaptation-induced mislocalizations (localization judgements (post) – localization judgements (pre)) of stationary and flashed bars during fixation.

Figure 5 about here

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 deg ± 0.22 (SE), flashed: 1.57 deg ± 0.21 (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 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 the study of Schnier & Lappe (2011), by establishing the link between these results and those of Zimmermann & Lappe (2009). Zimmermann & Lappe (2009) 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 (Deubel, 1999; Collins & Doré-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2007; 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 & Lappe, 2009).

Schnier & 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. Figure 4) this is exactly what we found. Also as expected, the absolute mislocalization of stationary bars was higher after outward adaptation than after inward adaptation (cf. Figure 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 & Lappe, 2010). Indeed, when inducing adaptation with a long-lasting post-saccadic visual error (Robinson et al., 2003) Zimmermann & Lappe (2010) revealed mislocalization during fixaton also after the inward adaptation procedure. In addition, the availability of post-saccadic target information also provided a contribution to the mislocalization, as seen by a larger amount of mislocalization in the target-on conditions in comparison to the target-off conditions for both inward and outward adaptation. Thus, the post-saccadic target is used as a visual landmark, but is responsible only for parts of the mislocalization (McConkie & Currie, 1996; Deubel et al., 2002; Awater & Lappe, 2006).

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; Ethier et al., 2008; Hernandez et al., 2008; Cotti et al., 2009; Panouilleres et al., 2009; Zimmermann & Lappe, 2010). Consequentely, this means that the differences in localization judgements 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 judgements of stationary bars, that 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 & 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 & 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 & Lappe (2010) obtained with flashed stimuli and extends them to stimuli that are continuously visible. The mislocalization during fixation may be explained if localization judgements during fixation use target registration or planning stages which 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 judgements 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 be also 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 judgements in common, namely the high amount of mislocalization of stationary bars (cf. Zimmermann & 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 be also 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 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 anti-saccades in the non-adapted direction (Cotti et al., 2009) suggesting a deep involvement of target registration or planning stages in the scanning adaptation procedure.

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Figure legends

Figure 1:

Timelines of the trials for the localization judgements 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 post-adaptation phase. The corresponding dashed lines indicate the timings in the pre-adaptation phase. The solid gray lines for T1 and T2 indicate target-off trials. T1 was 20 deg rightwards from FP. T2 appeared 6 deg leftwards or rightwards from T1, dependent on the experimental session (inward/outward). During fixation trials (B) a modified version of the fixation point 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 deg, height 2 deg, luminance 0.13 cd/m^2) was presented at a random position within an area 4 deg wide 2 deg high centered 2 deg directly above the target position T1. Subjects had to indicate the perceived bar position with a mouse pointer.

Figure 2:

Example sessions for the time course of saccadic inward (A) and outward (B) adaptation. The crosses indicate amplitude values in the pre-adaptation, adaptation, and post-adaptation 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 standard error. 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.

Figure 3:

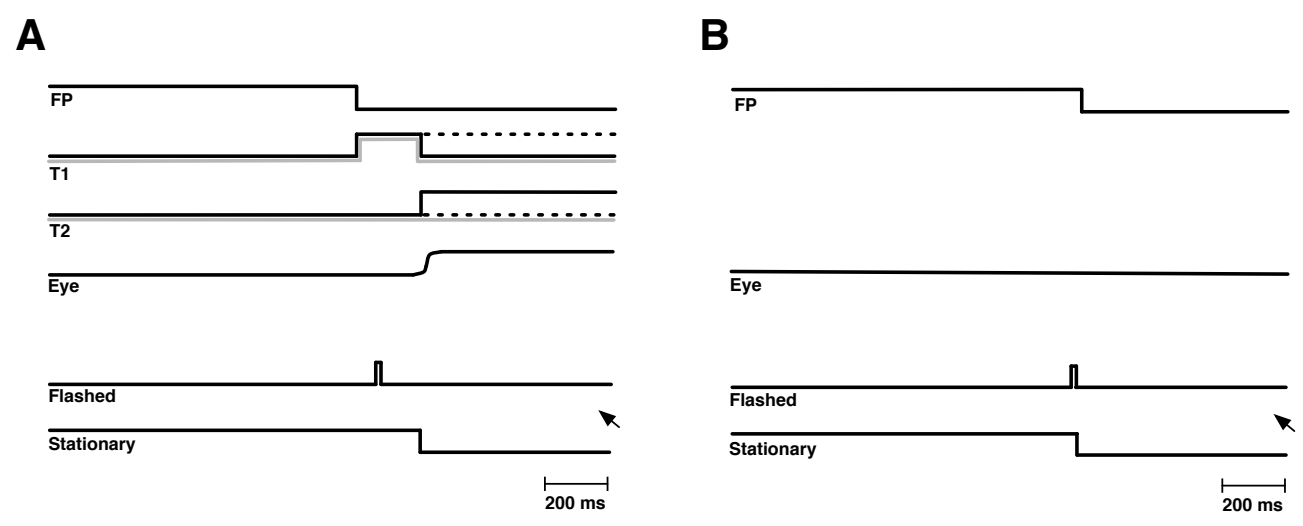
Adaptation-induced mislocalization of stationary (hatched bars) and flashed stimuli (solid bars) after inward (A) and outward (B) adaptation of reactive saccades. Dark gray bars indicate mean adaptation-induced mislocalizations in the target-on conditions. Light gray bars indicate mean mislocalizations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

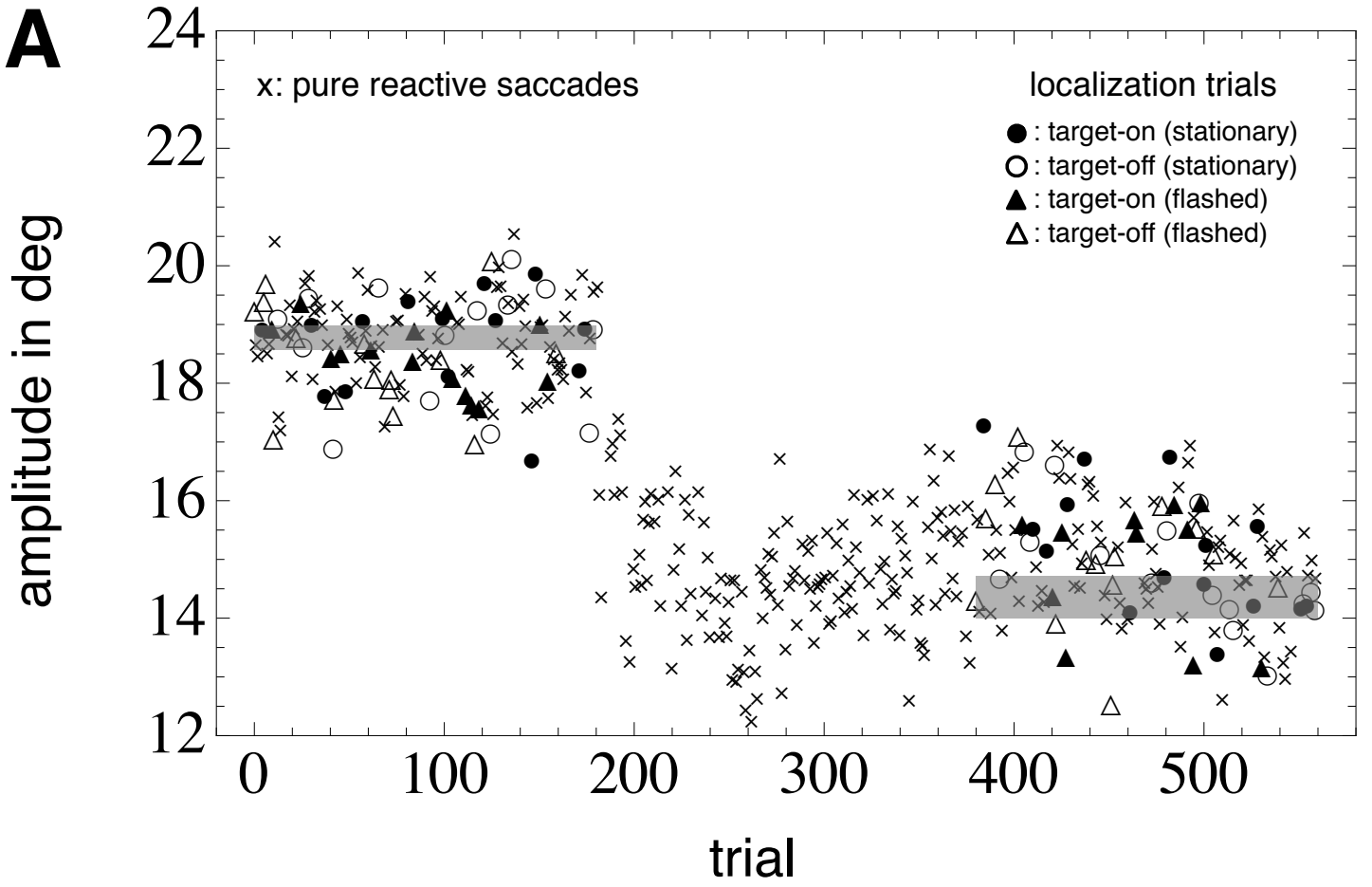
Figure 4:

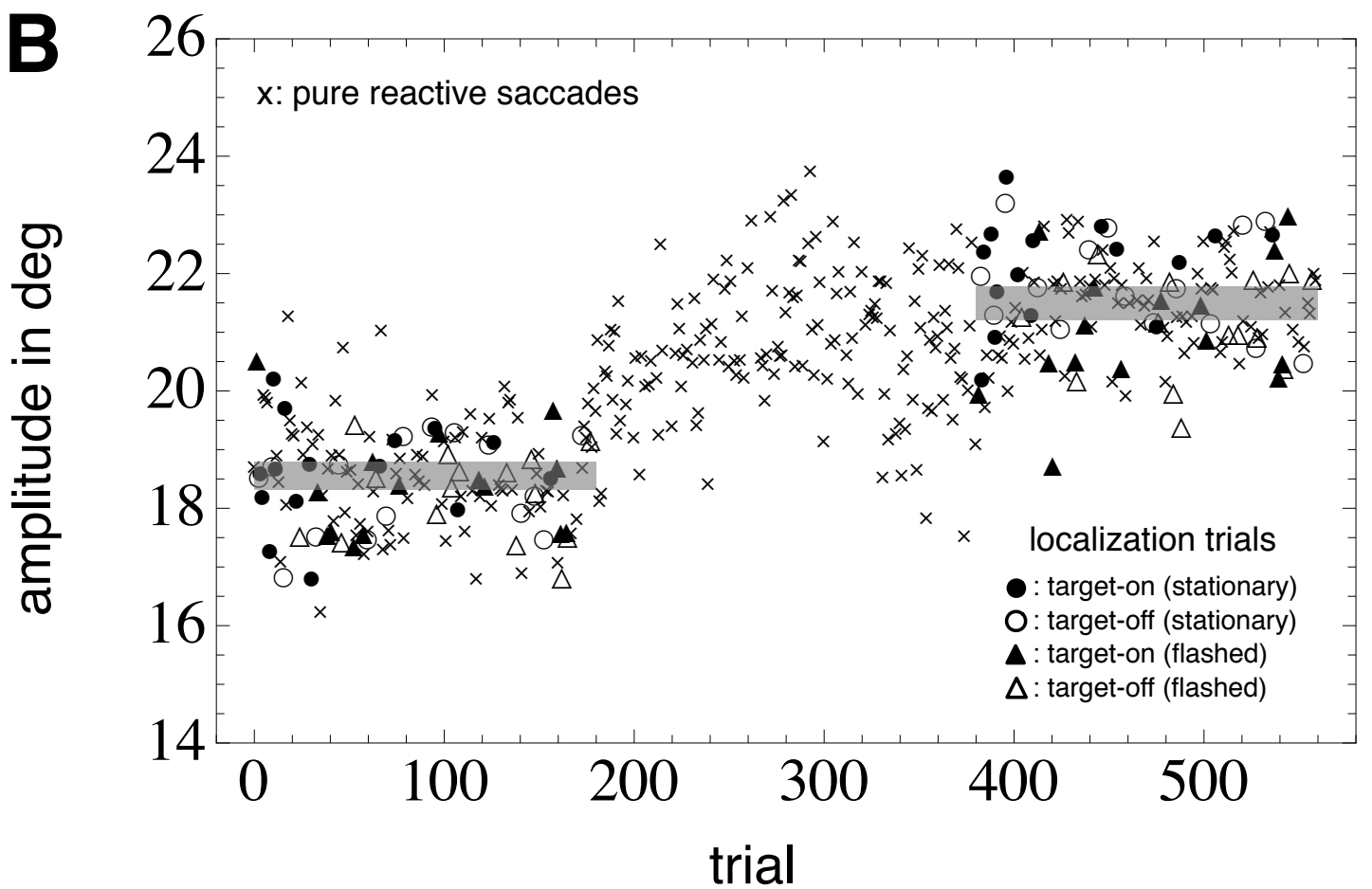
Percent ratio of adaptation-induced mislocalization of stationary bars in relation to flashed bars after inward (A) and outward (B) adaptation of reactive saccades (Dark gray: target-on, light gray: target-off). Percent ratio between the target-on conditions (inward: 37.9 %, outward: 86.3 %) as well 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 standard errors.

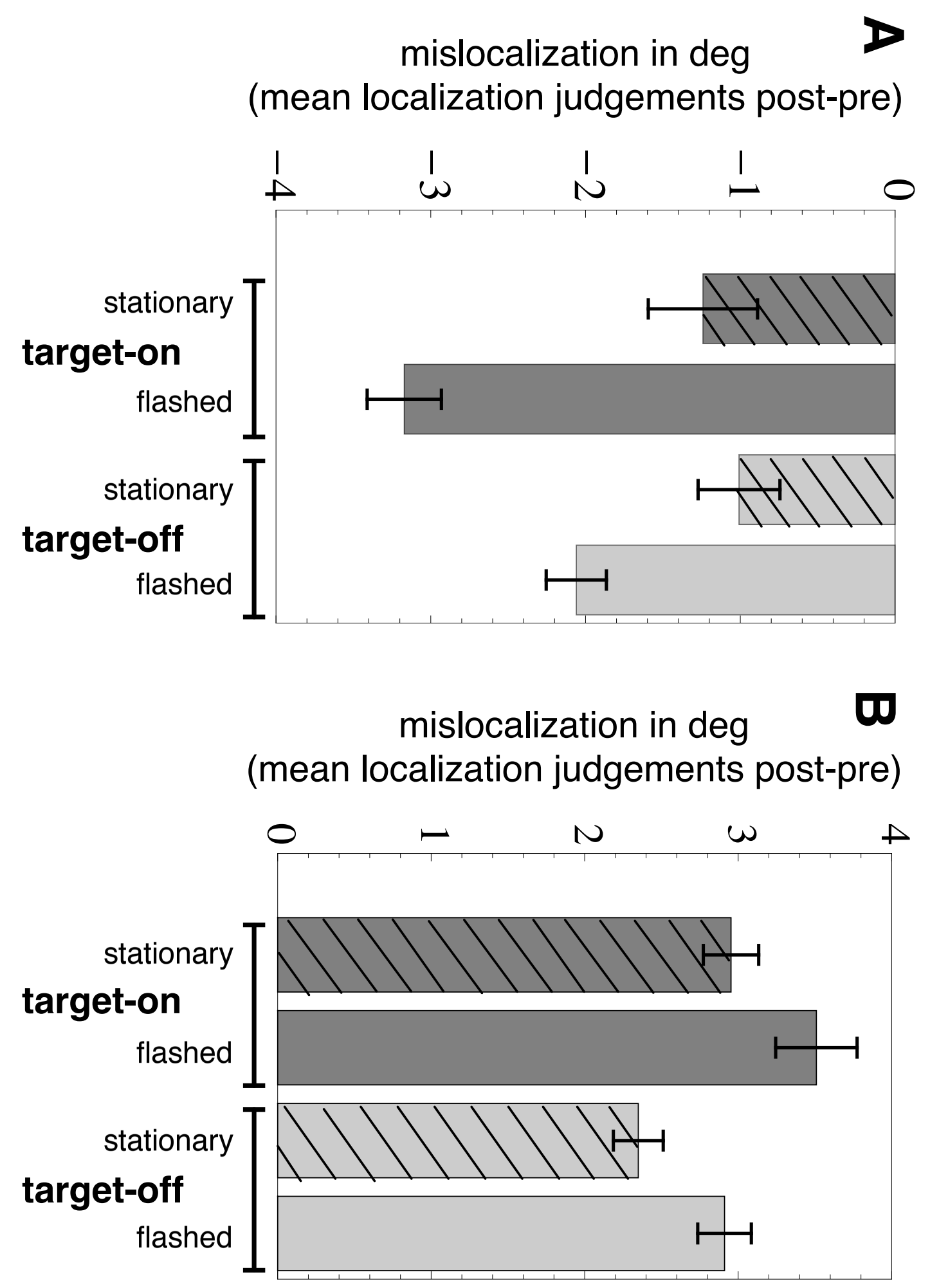
Figure 5:

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 standard errors.

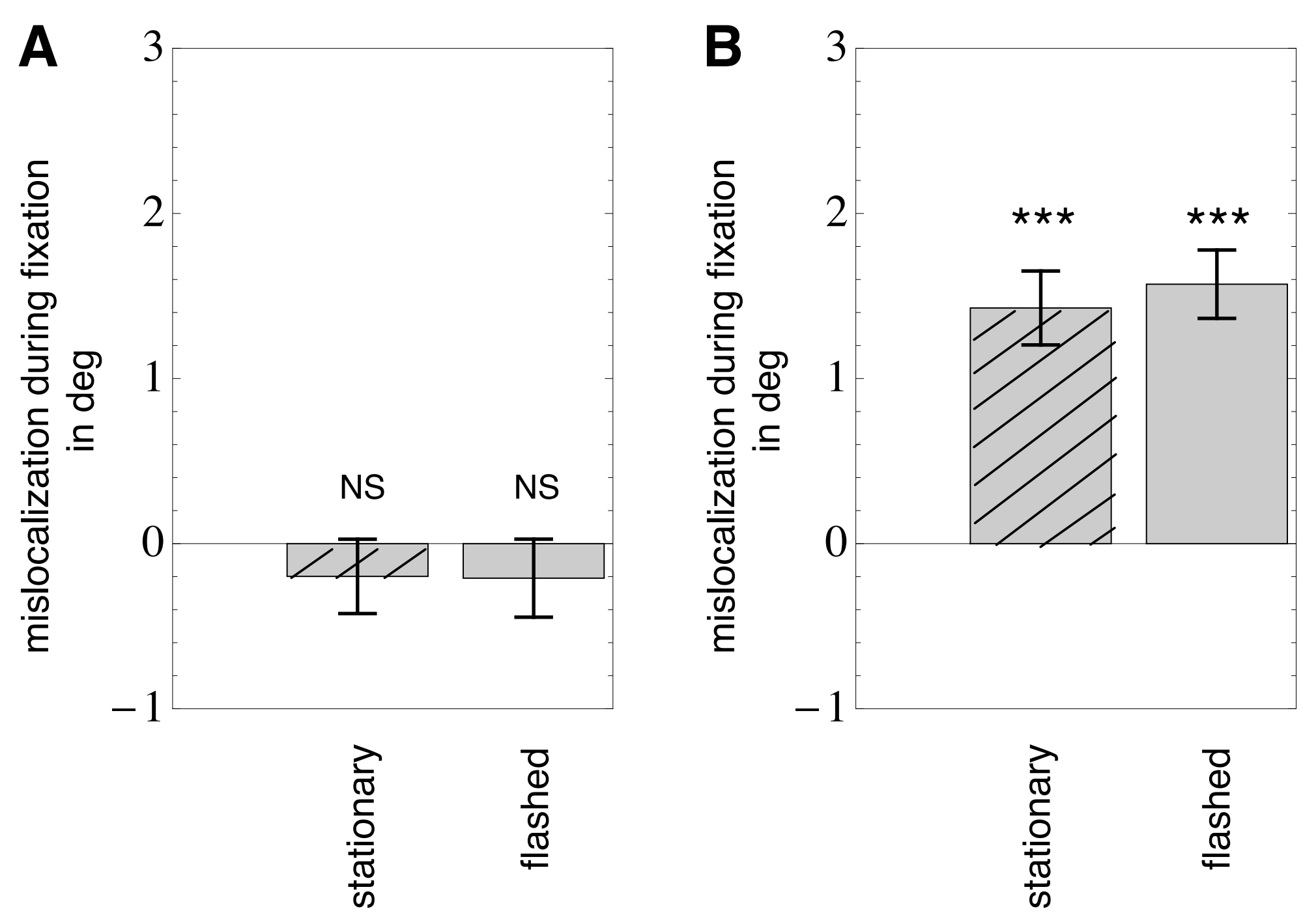

A
FP
T1
T2
Eye
Flashed
Stationary
200 ms
B
FP
Eye
Flashed
Stationary
200 ms


A
x: pure reactive saccades
localization trials
● : target-on (stationary)
○ : target-off (stationary)
▲ : target-on (flashed)
△ : target-off (flashed)
amplitude in deg
24
22
20
18
16
14
12
0
100
200
300
400
500
trial


B
x: pure reactive saccades
localization trials
● : target-on (stationary)
○ : target-off (stationary)
▲ : target-on (flashed)
△ : target-off (flashed)
amplitude in deg
26
24
22
20
18
16
14
0
100
200
300
400
500
trial


A
mislocalization in deg
(mean localization judgements post-pre)
4
3
2
1
0
stationary
target-on
flashed
stationary
target-off
flashed
B
mislocalization in deg
(mean localization judgements post-pre)
0
1
2
3
4
stationary
target-on
flashed
stationary
target-off
flashed

*
**
A
B
100
80
60
40
20
0
percent amount of mislocalization
(stationary/flashed) in %
target-on
target-off


A
B
3
2
1
0
−1
mislocalization during fixation
in deg
NS
NS
***
***
stationary
flashed