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Postsaccadic eye position contributes to oculomotor error estimation in saccadic adaptation

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Gremmler S, Lappe M. Postsaccadic eye position contributes to oculomotor error estimation in saccadic adaptation. *J Neurophysiol* 122: 1909–1917, 2019. First published September 18, 2019; doi: 10.1152/jn.00095.2019.—We investigated whether the proprioceptive eye position signal after the execution of a saccadic eye movement is used to estimate the accuracy of the movement. If so, saccadic adaptation, the mechanism that maintains saccade accuracy, could use this signal in a similar way as it uses visual feedback after the saccade. To manipulate the availability of the proprioceptive eye position signal we utilized the finding that proprioceptive eye position information builds up gradually after a saccade over a time interval comparable to typical saccade latencies. We confined the retention time of gaze at the saccade landing point by asking participants to make fast return saccades to the fixation point that preempt the usability of proprioceptive eye position signals. In five experimental conditions we measured the influence of the visual and proprioceptive feedback, together and separately, on the development of adaptation. We found that the adaptation of the previously shortened saccades in the case of visual feedback being unavailable after the saccade was significantly weaker when the use of proprioceptive eye position information was impaired by fast return saccades. We conclude that adaptation can be driven by proprioceptive eye position feedback.

NEW & NOTEWORTHY We show that proprioceptive eye position information is used after a saccade to estimate motor error and adapt saccade control. Previous studies on saccadic adaptation focused on visual feedback about saccade accuracy. A multimodal error signal combining visual and proprioceptive information is likely more robust. Moreover, combining proprioceptive and visual measures of saccade performance can be helpful to keep vision, proprioception, and motor control in alignment and produce a coherent representation of space.

adaptation; error signal; proprioceptive eye position; saccades

INTRODUCTION

For animals with mobile eyes, such as humans and nonhuman primates, retinal information about the environment has to be combined with proprioceptive signals of eye position in order to interact effectively with the world. Since only a very small part of the retina, the fovea, has a receptor density that is high enough for sharp vision, humans move their eyes very frequently to bring the next target of interest to this area of highest resolution of the retina. These fast eye movements are called saccades. To provide the required visual input of a targeted region fast and reliably to the visual system the intended landing position of the saccade needs to be reached accurately. Accuracy of the oculomotor system is maintained by a motor learning process called saccadic adaptation. When saccades systematically fail to reach their target, the saccade amplitude is adjusted in the way that it is shortened in face of hypermetric and lengthened in face of hypometric saccades (Hopp and Fuchs 2004; Pélisson et al. 2010). Saccadic adaptation can be induced in the laboratory by a shift of the saccade target during the eye movement. The saccade misses its target, and the saccade amplitude is modified such that it ends closer to the shifted target position.

Saccadic adaptation was found to be mainly driven by postsaccadic visual information, i.e., the difference between the expected retinal position of the target after the saccade and the actual retinal target position (Collins and Wallman 2012; Wallman and Fuchs 1998; Wong and Shelhamer 2011). Although vision provides reliable information of high accuracy, research on multisensory integration has often shown that precision can be increased by integrating other sensory signals (e.g., Alais and Burr 2004; Ernst and Banks 2002). For example, an estimate based on multisensory integration has lower variance than an estimate based on either visual or haptic information alone. In the case of saccadic adaptation, saccadic error estimates could become more precise if visual error information is combined with proprioceptive information on eye position after the saccade. This proprioceptive eye position information could be compared to the expected proprioceptive information for the intended final eye position, i.e., the eye position targeted by the motor command that steered the saccade. The use of proprioceptive eye position signals could enhance the efficiency and reliability of the adaptation mechanism. In the present study, we tested whether proprioceptive eye position information is used in saccadic adaptation. Several studies in the past reported that initial eye position signals modulate adaptation. For example, it is possible to adapt saccades of the same amplitude and direction differently when they start from different eye positions in humans (Alahyane and Pélisson 2004; Shelhamer and Clendaniel 2002) as well as in monkeys (Tian and Zee 2010). Beyond that, adaptation of saccades of the same amplitude and direction, and starting at a specific eye position, transfers only partially to other starting

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eye positions in humans (Gremmler and Lappe 2016; Havermann et al. 2011; Zimmermann et al. 2011; Zimmermann and Lappe 2011) and monkeys (Wulff et al. 2012). Furthermore, during head-free gaze movements, the target command for saccadic adaptation is in gaze coordinates, not in retinal coordinates (Cecala and Freedman 2008, 2009). Collectively, these studies show that proprioceptive eye position information about the starting eye position is available to the adaptation mechanism. In the present study we wanted to test whether proprioceptive eye position information about the landing eye position provides a motor error signal that can drive adaptation. A multimodal input to the adaptation mechanism that includes a proprioceptive error signal could provide independent information when visual feedback is unreliable or unavailable. Furthermore, if visual and proprioceptive signals are both considered during adaptation, this may help to keep visual and extraretinal information in register with each other. Since both signals have to be combined in spatial perception, the maintenance of a coherent percept of the visual space (Zimmermann and Lappe 2016) could also be facilitated.

We know that postsaccadic visual feedback offers a strong learning signal that generates fast and persistent adaptation (Hopp and Fuchs 2004; Pélisson et al. 2010; Wong and Shelhamer 2011). Hence, the most direct way to test for an effect of the eye position signal on saccadic adaptation would seem to be to eliminate the visual feedback after the saccade and then see if adaptation can be induced solely based on proprioceptive feedback. However, to generate motor learning after the saccade from the proprioceptive eye position there needs to be a mismatch between the expected or intended postsaccadic eye position and the actual landing position. In the standard adaptation paradigm with visual error, such a mismatch is created by shifting the target during the saccade. Unfortunately, it is more difficult to induce such a mismatch between the intended postsaccadic eye position and the actual postsaccadic eye position because we cannot manually shift the postsaccade eye position. In the present study, we instead induced the mismatch by decreasing the saccade amplitude beforehand through conventional visual error-driven adaptation. After such initial adaptation, the saccade does not bring gaze directly to the previously perceived peripheral target position anymore. Thus the saccade does not end with the intended postsaccadic eye position, either. If our hypothesis is correct and saccadic adaptation monitors the accuracy of the saccade by a comparison between the intended and observed postsaccadic eye position, we should see a regression of the visually induced amplitude modifications even when no visual feedback is provided after the saccade.

Since in this paradigm the amplitude is approaching the state it has had before the first adaptation, this second adaptation is sometimes called deadaptation. In conventional adaptation paradigms, deadaptation occurs after prior adaptation when the intrasaccadic target jump is abolished and the target stays at the same position before and after the saccade. In this case, postsaccadic visual error gradually returns the amplitude to the preadaptation baseline. If the target does not stay in place across the saccade but is instead switched off during the saccade, a return to baseline has also been observed but with a slower time course (Seeberger et al. 2002). Hence, when the target is visible and expedites deadaptation, the visual feedback actively contributes to the adaptation back to the preadaptive

state. Therefore, the adaptation that brings the amplitude to the baseline state includes a component that modifies the amplitude according to visual error signals rather than being the consequence of a simple passive return to the baseline state (Ethier et al. 2008; Kojima et al. 2004).

The fact that this deadaptation or secondary adaptation occurs more slowly also in the absence of visual feedback is a promising indication that the process may include a second, less effective, error signal. In our study, we tested whether saccadic adaptation without visual feedback is an active process based on a nonvisual error signal by comparing the amplitude changes that evolve during secondary adaptation when the target is switched off to the amplitude changes that evolve during a period of fixation of the same duration. If saccade amplitude change during the repeated execution of saccades without postsaccadic visual feedback is stronger than any amplitude change during fixation, an error signal other than visual error must be involved.

Furthermore, we wanted to test whether this error signal is provided by proprioceptive eye position information. To manipulate the availability of proprioceptive eye position information, we restricted the time that is available for the estimation of the error by introducing the protocol of fast return trials. In those trials, participants were instructed to saccade back to the fixation point as fast as possible after they accomplished the main saccade to the target. The fast execution of the return saccade results in a very brief retention time of gaze in the target area. Normal saccadic adaptation with visual feedback is known to occur with short retention times (Gray et al. 2014). However, a short retention time likely interferes with successful acquisition of the proprioceptive feedback, since the proprioceptive eye position information builds up gradually over time. A number of studies found that the time needed for proprioceptive eye position information to develop completely is of the same magnitude as typical saccade latencies, i.e., 200–300 ms. Wang et al. (2007) reported that the tonic signal that represents orbital eye position in neurons of the monkey's primary somatosensory cortex is overlaid by a phasic excitation during saccades such that during the 300 ms following the end of the saccade eye position information is inaccurate and unreliable. Furthermore, eye position neurons in area 3a of somatosensory cortex reflect changes in eye position during smooth pursuit with an average latency of ~60 ms, whereas some neurons even show latencies > 100 ms (Xu et al. 2011). Tanaka (2007) found that eye position-related neurons located near the dorsal surface of the central thalamus discharge with a latency of 120 ms (SD 88 ms) after an eye movement. For vision-related cortical areas, Morris et al. (2012) found that eye position signals in the lateral intraparietal area (LIP), the ventral intraparietal area, the middle temporal area, and the medial superior temporal area stabilize as late as 150 ms after a saccade. Furthermore, the authors showed that the activity in the population of LIP neurons during a saccade can be used to calculate an eye position signal that resembles the actual eye position with a temporal lag of ~200 ms. While investigating the time course of eye position gain fields in the parietal cortex, Xu et al. (2012) found that 50 ms after an eye movement most neurons in the LIP still show a response reflecting the presaccadic eye position instead of the actual postsaccadic eye position. Additionally, the authors found that the majority of neurons with eye position gain fields in area LIP did not show

the predicted postsaccadic steady-state response until as late as 250 ms after the saccade. The remainder of the neurons were found to show the responses that were predicted by the steady-state gain fields by 350 ms after the execution of a saccade. The origin of the visual response modulating eye position signal in the parietal cortex is still unknown, but the slow time course seems to be more consistent with the timing of the proprioceptive eye position signal in area 3a and the LIP gain fields described by Morris et al. (2012) than an efference copy signal of the motor command, which should be available with little or no time lag. Afferent signals from the extraocular eye muscles are also available in the cerebellum (Donaldson 2000; Fuchs and Kornhuber 1969), an important structure for saccade adaptation (Optican and Robinson 1980; Pélisson et al. 2010). These afferent signals can be detected with short latency in the cerebellar vermis, but their functional role has been difficult to determine (Donaldson 2000), as signals from stretched muscles do not directly lead to a representation of current eye position. Thus the electrophysiological data in summary indicate that a reliable proprioceptive eye position signal might not be available for comparison with the expected eye position until 200–300 ms after the saccade. Hence, our fast return trials might not allow the system to estimate eye position properly after the first saccade and, if so, should prevent a process of proprioceptive saccadic adaptation from completing.

Proprioceptive eye position information is very likely also used for recalibration of spatial coordinates during saccades. Since the recalibration is a time-critical process to maintain visual stability, its time course provides further information about the availability of a reliable eye position signal. Grüsser et al. (1987) developed a computational model for the recalibration of retinal coordinates and fitted psychophysical data of perceived afterimage movement during saccades in the dark with a two-stage linear filter. The time constant of the recalibration was found to be 90–120 ms and the dead time in the range of 180–330 ms, consistent with the later electrophysiological studies described above. In more recent work, Ziesche and Hamker (2011) developed a computational model for perisaccadic spatial representation in the LIP. In this model, LIP neurons, which are modulated by the postsaccadic proprioceptive signal, start to respond 50 ms after a completed saccade, whereas the presaccadic proprioceptive signal needs some time to decay after the saccade. This results in a delay such that on the population level the correct representation of eye position is restored ~200 ms after the saccade. Importantly, the authors show that supplanting this mechanism with information from an efference copy signal of the eye movement can provide an accurate perisaccadic spatial representation with no time lag. However, an efference copy signal cannot be used to estimate movement error, i.e., to compare the saccade outcome with the predicted outcome, since the efference copy is itself a predictive signal and hence not suitable to verify the predicted postsaccadic situation.

In the present study we aimed to investigate whether the proprioceptive eye position signal after the execution of a saccadic eye movement is used to estimate the motor error and to drive saccadic adaptation. To induce a mismatch between intended and perceived postsaccadic eye position, we first decreased the saccade amplitude in a conventional adaptation paradigm.

MATERIALS AND METHODS

Subjects were students and members of the Institute of Psychology of the University of Münster. Students' participation in the experiment was recompensed with study points required for successful graduation. In total 10 subjects (5 men, 5 women) participated, with a mean age of 30.5 (SD 10.0) yr. All subjects had normal or corrected to normal vision and gave written informed consent to participation. The experiment design was approved by the ethics committee of the Department of Psychology and Sport Science of the University of Münster.

Recording of Eye Movements and Stimulus Presentation

Eye movements were recorded with an EyeLink 1000 system (SR Research, Ontario, Canada) with a frequency of 1,000 Hz. Viewing was binocular while the right eye was recorded. The stimuli were presented on an Eizo FlexScan 22-in. monitor (Eizo, Hakusan, Japan) with a display resolution of 1,152 × 864 pixels and a refresh rate of 75 Hz. The participants were seated with the head in a chin rest at a distance of 57 cm in front of the monitor in a completely dark room. A transparent foil covered the display and reduced the maximum luminance of the display from 54.1 cd/m² to 3.2 cd/m². Experimental control and data analysis was performed in MATLAB (MathWorks, Natick, MA) with the Psychophysics Toolbox extension (Brainard 1997; Kleiner et al. 2007).

Behavioral Task

Stimuli were round dots with a diameter of 0.5°. Every trial started with the presentation of a white fixation point at the center of the screen. After a random interval of 400–900 ms a red target point was presented 11° to the right of the fixation point. The subjects were instructed to saccade to the target as soon as it appeared. Every session started with 20 preadaptation trials in which the target remained at its position for 1 s after the saccade to the target was completed so that the subject had sufficient time to receive visual feedback after the saccade. Thereafter, the target disappeared and the screen was empty for 1 s before the next trial started. The primary adaptation phase started with *trial 21* and lasted for 100 trials. During this phase, the saccade target was shifted 3° backward against saccade direction after saccade onset, i.e., when the eye velocity exceeded 138°/s. The target remained at its new position for 1 s. The target shift led to an amplitude decrease such that saccades landed closer to the position of the shifted target. After the end of the primary adaptation phase, when saccade amplitude had reached a stable level the secondary adaptation phase started, in which the target ceased to jump during the saccade. This was the main experimental phase in which we measured saccade changes back to the preadaptation amplitude in five experimental conditions that manipulate the availability of visual and proprioceptive feedback. The five types of adaptation trials in this secondary adaptation phase are described below (see also Fig. 1).

Target-on condition. In the target-on condition (ON) we measured amplitude modification during conventional deadaptation for comparison with the other conditions. Trials in this condition resembled the preadaptation trials. The target was not shifted but remained in its first position at 11° horizontal gaze angle for 1 s after the saccade. Hence visual feedback was available after the saccade and could be used to readapt to the preadaptation amplitude.

Target-off condition. In the target-off condition (OF), the target was switched off as soon as the saccade onset was detected, so that no visual feedback was available after the saccade. Proprioceptive feedback from the final eye position may be used in this condition.

Target-off-return condition. In the target-off-return condition (OFR), the target was switched off at saccade onset and simultaneously the fixation point was switched back on for 300 ms. The subjects were instructed to make a saccade back to the fixation point as fast as
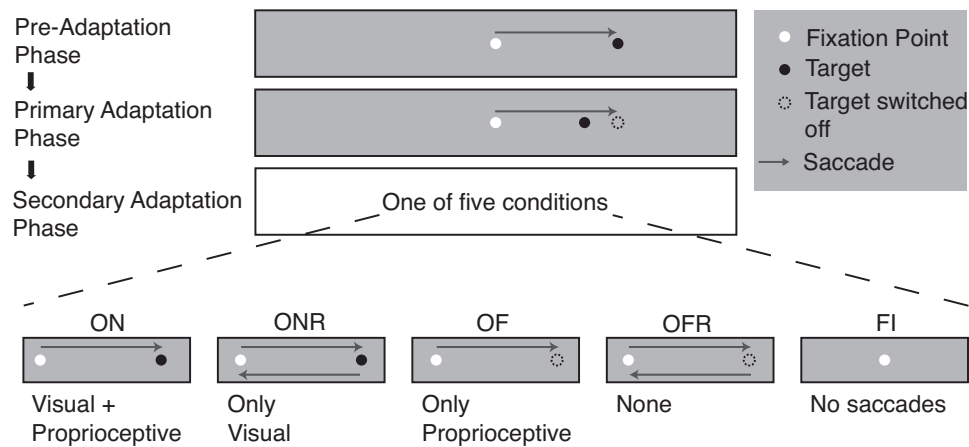
Fig. 1. Every subject participated in 5 sessions, and each session consisted of 3 phases: preadaptation, primary adaptation, and secondary adaptation, the last containing the experimental manipulation. The preadaptation phase and the primary adaptation phase were identical in all conditions. The secondary adaptation phase presented different adaptation trials in each of the 5 conditions. Target on (ON): the target remained in place during the saccade and was visible for 1 s after the saccade. Target-on-return (ONR): the target remained in place and was visible after the saccade, but subjects were instructed to make a return saccade back to the fixation point immediately after the saccade to the target. Target off (OF): the target was switched off during the saccade. Target-off-return (OFR): the target was switched off during the saccade, and subjects were instructed to make a return saccade back to the fixation point immediately after the saccade to the target. Fixation (FI): the subjects held fixation and did not conduct any saccades for a period of time that equaled the duration of the other 4 adaptation phases. The available error information in each condition is indicated at *bottom*.

possible after landing in the target area. The fast return saccade restricted the availability of proprioceptive eye position information of the landing point of the first saccade, since proprioceptive signals need time to develop after a saccade.

Target-on-return-condition. In the target-on-return condition (ONR), subjects were also requested to make a fast return saccade, but the target remained in place after the saccade such that visual feedback was available. Fixation point and target were both switched off 300 ms after the first saccade. This condition was included to control whether the fast return saccade itself would interfere with adaptation, even when visual error, the main driving signal for adaptation, is available.

Fixation condition. In the fixation condition (FI), subjects did not perform any saccade. Instead, they had to keep fixation on the fixation point in the screen center for 234 s, the duration of the other conditions. This condition measured the amount of deadaptation to preadaptation baseline level that would occur without any saccade activity or visual or proprioceptive error signals. To test the adaptation state after the fixation time, 20 target-off trials followed the fixation interval.

The order in which the five conditions were accomplished by the subjects was counterbalanced. Measurements of different conditions were separated by at least 1 wk to prevent any influence of the adaptation in the preceding measurement.

Data Analysis

Start and end of saccades were tagged in the off-line analysis when eye velocity exceeded (start) or dropped below (end) 30°/s and acceleration exceeded or fell below 8,000°/s². Saccade amplitude was calculated for every trial in every condition for every subject. Trials in which the primary saccade amplitude was smaller than 5.5° or larger than 16.5° were considered not directed toward the target and were omitted from analysis. Similarly, trials in which the saccade latency after target presentation was either shorter than 100 ms or longer than 400 ms were discarded. Over all conditions an average of 89.8% (SD 0.02%) of trials contained a valid primary saccade. The 20 preadaptation trials were used to calculate a preadaptation amplitude for every single subject in every condition. The last 20 trials of the primary adaptation phase were used to calculate the mean amplitude at the end of the primary adaptation. Likewise, the last 20 trials of the secondary

adaptation were used to calculate the mean amplitude in each of the five experimental conditions.

RESULTS

Figure 2 presents the grand average of amplitude development, i.e., the mean amplitude of all subjects in every trial, for the five conditions. The grand average curves show the saccade amplitudes in each of the three phases: preadaptation, primary adaptation, and secondary adaptation. In the primary adaptation phase, the saccade amplitudes decrease similarly in all conditions because of the target shift against saccade direction. In the secondary adaptation phase, in contrast, amplitude changes differ between the conditions. To investigate potential differences in the amount of adaptation in this phase between the conditions we analyzed the mean preadaptation (Fig. 3*A*), primary adaptation (Fig. 3*B*), and secondary adaptation (Fig. 3*C*) amplitudes over all subjects in the five conditions. Since all five sessions were identical until the secondary adaptation phase started and since the subjects accomplished the sessions in a counterbalanced order, we expected similar levels of preadaptation amplitude and of primary adaptation amplitude in all conditions. Consistent with this expectation, two one-way ANOVAs showed no influence of condition on either the preadaptation amplitudes [$F(4,45) = 0.1$, $P = 0.98$] or the end-of-adaptation amplitudes [$F(4,45) = 0.16$, $P = 0.96$].

The experimental manipulations were applied in the secondary adaptation phase. We expected differences between conditions in the amplitudes reached at the end of the secondary adaptation. Consistent with this expectation, a one-way ANOVA found a significant effect of condition on the amplitudes after secondary adaptation [$F(4,45) = 8.26$, $P = 0.00004$].

For further analysis, reported below, we determined whether the amplitudes in conditions ON, ONR, OF, and OFR were different from the amplitudes in condition FI, which served as a baseline without active secondary adaptation. We also determined the relation between the amplitudes in conditions ON and ONR. All of these comparisons used post hoc *t* tests with Bonferroni-adjusted α levels of 0.01 per test (0.05/5).
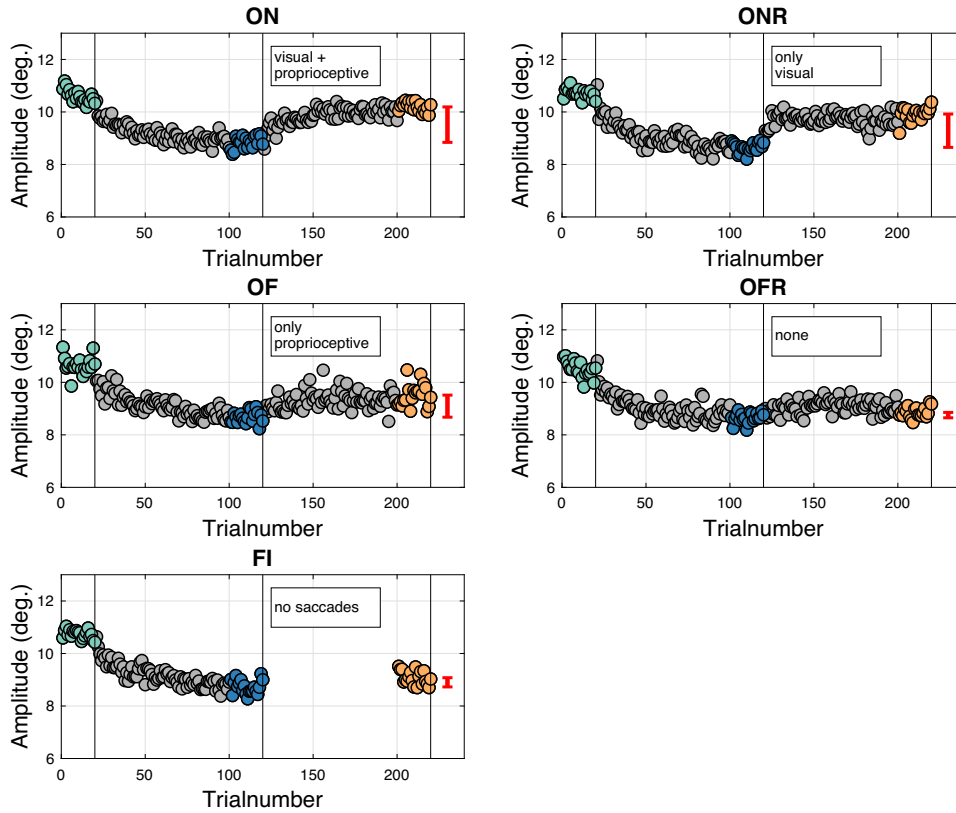
Fig. 2. Each panel presents the grand average adaptation time courses over all subjects for each condition. The amplitudes in the first 20 trials (*trials 1–20*, green dots) were used to calculate the preadaptation amplitude. The amplitudes in the last 20 trials of the primary adaptation phase (*trials 101–120*, blue dots) were used to calculate the adaptation state achieved at the end of the primary adaptation phase. The amplitudes in the last 20 trials of the secondary adaptation phase (*trials 201–220*, orange dots) were used to calculate the adaptation state achieved at the end of the secondary adaptation phase. In condition FI, 20 target-off trials (orange dots) were conducted after the extended fixation time of 234 s to measure the adaptation state after the period of fixation. Red lines on *right* of each panel indicate the amount of adaptation achieved during the secondary adaptation phase, i.e., the difference between the blue and orange dots. ON, target on; ONR, target-on-return; OF, target off; OFR, target-off-return; FI, fixation.

In the Absence of Visual Feedback, Active Adaptation Still Occurs When the Eye Stays at the Target Location for an Extended Period of Time

In condition OF, no visual feedback was provided but the development of proprioceptive feedback was not impeded. Average secondary adaptation amplitude was 9.5° (SD 0.4°), which is different from the secondary adaptation amplitude in fixation condition FI of 9.1° (SD 0.5°) (2-tailed paired *t* test, $P < 0.004$). Thus the execution of saccades during the secondary adaptation with proprioceptive but no visual feedback

induced stronger amplitude changes than a pure period of fixation. Hence, the mismatch between the intended and the perceived eye position after the executed saccades in condition OF induced saccadic adaptation.

In the Absence of Visual Feedback, Active Adaptation Does Not Develop When the Eye Quickly Returns to the Fixation Point

In condition OFR, no visual feedback was available after the saccade and the availability of proprioceptive feedback was
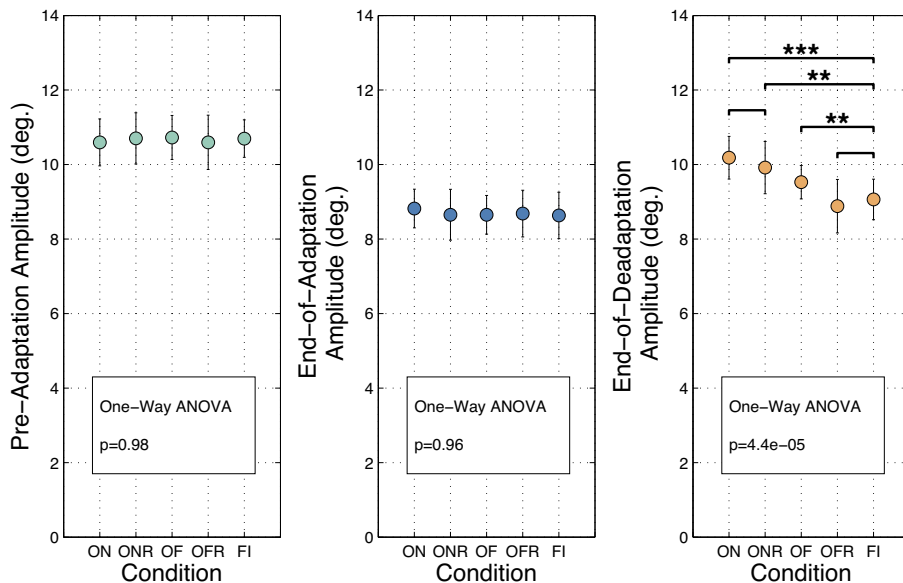

Fig. 3. Grand average amplitudes over all subjects in the 5 conditions [target on (ON), target-on-return (ONR), target off (OF), target-off-return (OFR), and fixation (FI)] for the preadaptation trials (*left*), the primary adaptation trials (*center*), and the secondary adaptation trials (*right*). **$P < 0.01$; ***$P < 0.001$.

impeded by the fast return of the gaze to the fixation point. The secondary adaptation amplitude was 8.8° (SD 0.6°) and thus not longer than the amplitude in fixation condition FI of 9.1° (SD 0.5°) (1-tailed paired *t* test, *P* = 0.75). Hence, the execution of the saccades during the secondary adaptation phase did not produce any active amplitude change when neither visual nor proprioceptive feedback was available. Sufficient dwell time seems to be necessary for the proprioceptive signal to build up and be used for the adaptation mechanism.

Conditions with Visual Feedback Induce Strong Adaptation, Irrespective of Whether the Eye Returns Quickly to the Fixation Point or Remains at the Target for a Longer Time Period

In condition ON, which resembles conventional deadaptation, visual feedback and proprioceptive feedback are both available after the saccade. The average secondary adaptation amplitude was 10.2° (SD 0.6°), significantly different from that in condition FI (2-tailed paired t tests, *P* < 0.001). In condition ONR, visual feedback was available but proprioceptive feedback was impaired. In this condition, the secondary adaptation amplitude was 9.9° (SD 0.7°), again significantly different from condition FI (2-tailed paired *t* tests, *P* < 0.004). Amplitudes in conditions ON and ONR did not differ significantly from each other (2-tailed paired *t* test, *P* = 0.12). Thus the execution of the saccade during the secondary adaptation phase together with visual error feedback induced stronger secondary adaptation than the period of fixation in condition FI, but in the presence of visual feedback the availability of proprioceptive feedback seems to be dispensable. Importantly, we do not see any evidence that a long dwell time is required for successful saccadic adaptation when visual feedback is available.

Latency of Return Saccades in ONR/OFR Conditions Is Lower than in ON/OF Conditions

We clearly found an influence of the execution of fast return saccades on the amount of adaptation in the secondary adaptation phase. To validate that this result is related to the dwell time needed for the development of the proprioceptive eye position signal, we compared latencies of return saccades in the ONR/OFR and ON/OF conditions. We calculated latency of a return saccade as the time between the end of the primary saccade and the start of the return saccade. Figure 4 shows latency distributions for the four conditions. The percentage of return saccades with a latency smaller than 300 ms was 71% in condition ONR and 51% in condition OFR, whereas the number of return saccades with such latencies below 300 ms is negligible in conditions ON and OF (Figure 4). Hence, the dwell time in the majority of fast return saccades in conditions ONR/OFR was below the range in which the proprioceptive eye position signal appears fully developed, whereas almost all trials in conditions ON and OF had dwell times long enough for the proprioceptive eye position signal to contribute to error estimation.

Taken together, the differences in amplitude development between conditions OF and FI does clearly show that in condition OF active adaptation is involved. To test whether the proprioceptive eye position signal is a sufficient learning signal that can drive saccadic adaptation, we measured two control conditions in which the availability of the proprioceptive eye position signal was impaired through restricted dwell time at the target gaze location (ONR and OFR). Since there was no difference between conditions OFR and FI, sufficient dwell time is needed so that active adaptation can emerge. This dwell time is not needed for adaptation per se, since visual error-based adaptation in condition ONR occurs even for fast return saccades. In condition OFR, however, the fast return saccades prevent adaptation, consistent with our hypothesis that the postsaccadic eye position signal is used in adaptation but is only available after sufficient dwell time.

Corrective Saccades During the Secondary Adaptation Phase

We next analyzed corrective saccades during the secondary adaptation phase. In conditions in which the target is stepped during the primary saccade, corrective secondary saccades are expected to compensate for the target shift and bring gaze to the new target position. In the present study, however, subjects
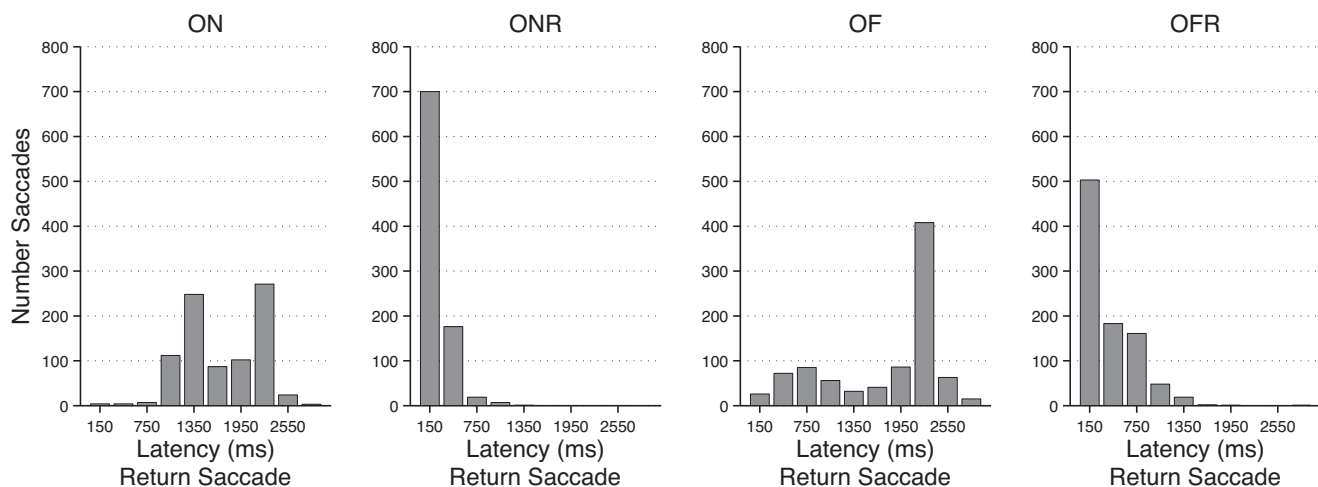

Fig. 4. Distribution of the latency of the return saccades in bins of 300 ms for all 4 conditions containing adaptation trials [target on (ON), target-on-return (ONR), target off (OF), and target-off-return (OFR)]. The first bar of each plot shows the number of saccades with latencies shorter than 300 ms. Although the number of return saccades with such short latencies is negligible in condition ON and condition OF, more than half of the return saccades in the fast return conditions ONR and OFR have latencies shorter than 300 ms.

were instructed in some conditions to perform fast return saccades in the secondary adaptation phase. In this case, return saccades instead of corrective saccades may be expected. However, if participants fail to comply with the instruction one may also expect a corrective saccade instead of or in addition to the return saccade. To analyze this, we defined corrective saccades as secondary saccades occurring after the primary saccade with an amplitude of up to 3°, i.e., the previously adapted target step size. In condition ON, there was a high mean rate of corrective saccades [89.2% (SD 8.8%)], as expected. In condition ONR, in which participants were asked to immediately return to the fixation point, the mean rate of corrective saccades to the target was low [14.2% (SD 17.9%)], indicating that participants followed instructions. Importantly, since there was no difference in adaptation between conditions ON and ONR, the differences in rate of corrective saccades did not affect the adaptation. This is in line with Wallman and Fuchs (1998), who also reported that corrective saccades had little role in adaptation. In condition OFR, as in condition ONR, participants made very few corrective saccades [10.4% (SD 16.0%)] and complied well with the instruction to return immediately to the fixation point, to eliminate the proprioceptive signal. In condition OF, however, corrective saccades occurred on average in about half of the trials [48.3% (SD 24.2%)], even though no visual error was present. These corrective saccades in condition OF, however, had unusually long mean latencies [599.0 ms (SD 197.4 ms)], much longer than those in condition ON [average: 205.9 ms (SD 59.6 ms), paired t test, $P < 0.0001$]. Thus these corrective saccades did not abolish the proprioceptive signal since the eye remained at the target location long enough for the signal to develop. Therefore, the long latency of the corrective saccade supports the view that the proprioceptive signal replaces the visual error in condition OF. To perform a corrective saccade in this condition, the oculomotor system would first have to establish an error based on the slow proprioceptive information. The latency of the corrective saccade is very much in line with the time course of the proprioceptive signal that can be assumed based on the available electrophysiological data.

DISCUSSION

Saccadic eye movements, the most frequent movement we make, pose multiple challenges to sensorimotor control and perception. First, since they are too fast to allow closed-loop visual feedback control, their kinematics must be programmed in advance. Errors in this programming must be determined after the saccade and used to adjust the program for future saccades by saccadic adaptation. Second, since saccades disrupt visual continuity, the perceptual system needs to match presaccadic and postsaccadic images to allow stable visual perception. Third, since not only the eyes but also the head is movable, vision needs to be combined with information about eye-in-head position to maintain a globally consistent percept of the world and the action. Previous studies on the nature of the error signal that drives saccadic adaptation indicated that vision provides the main source (Collins and Wallman 2012; Wallman and Fuchs 1998; Wong and Shelhamer 2011). However, research on multisensory perception has often found that a combination of sensory signals is more precise than any one signal alone (Alais and Burr 2004; Ernst and Banks 2002). Our

results show that proprioceptive eye position signals, in addition to vision, provide a source of motor error estimation for saccadic adaptation.

Several studies in the past had shown that proprioceptive eye position signals modulate adaptation (Alahyane and Pélisson 2004; Cecala and Freedman 2008, 2009; Havermann et al. 2011; Shelhamer and Clendaniel 2002; Zimmermann et al. 2011; Zimmermann and Lappe 2011). However, none of these studies tested whether eye position contributed to the evaluation of the postsaccadic error itself. Yet, the inclusion of postsaccadic proprioceptive feedback in the error estimation for the adaptation mechanism not only has the advantage that a multimodal-based mechanism can be more reliable, it may furthermore help to keep visual and extraretinal information in register with each other during oculomotor learning.

In the present experiment we tested whether saccadic adaptation can be driven by proprioceptive feedback in the absence of visual feedback. Therefore, we induced a mismatch between the intended postsaccadic eye position and the observed postsaccadic eye position, just like in conventional adaptation, where the jump of the visual target induces a mismatch between the expected postsaccadic retinal target position and the observed postsaccadic target position. We induced the mismatch of intended and observed eye position by first modulating the saccade amplitude via conventional visual error-based saccadic adaptation such that the saccade ended with an eye position that differed from the intended target position. Afterwards, in a second adaptation phase, we measured amplitude changes when saccades were executed with and without visual feedback, with full and with limited proprioceptive feedback, and when no saccades were executed at all. We found that the amount of this secondary adaptation was strongest with visual feedback available (conditions ON and ONR), still present when visual feedback was unavailable but proprioceptive eye position was available (condition OF), and nonexistent when neither visual nor proprioceptive feedback was available (condition OFR). In the latter case, the amount of adaptation was equal to the amplitude change that emerged after a period of fixation, i.e., to a passive decay of prior adaptation (condition FI).

In condition OF, no postsaccadic visual feedback was available in the second adaptation phase since the target was switched off during the saccade. Despite the absence of any visual error signal, the saccade amplitude gradually became longer than during the pure fixation period in condition FI. Hence, we conclude that the observed amplitude change in condition OF is not the consequence of a passive returning of the system to a default baseline state but shows an active process not relying on visual feedback. To test whether proprioceptive eye position provides the error signal that drives this process we measured two further experimental conditions. In these conditions, we manipulated the availability of the proprioceptive eye position signal. First, in condition OFR we impaired the postsaccadic access to proprioceptive eye position signals by a protocol of fast return saccades. Since the proprioceptive eye position signal builds up slowly after the saccade (Grüsser et al. 1987; Honda 1991; Morris et al. 2012; Tanaka 2007; Wang et al. 2007; Xu et al. 2011, 2012), a reliable proprioceptive eye position signal should not be available to the adaptation mechanism within the latency of a fast return saccade (200–300 ms). Since 51% of fast return saccades had

latencies below 300 ms, a sizable number of trials would have missed a reliable proprioceptive error signal. The lack of adaptation in this condition hence shows that postsaccadic proprioceptive eye position provides an error signal for saccadic adaptation. Second, in the ONR condition we also impaired postsaccadic access to proprioceptive eye position signals through return saccades but added visual error signals. This condition was included to show that the fast return protocol itself did not impair adaptation. The adaptation obtained in the fast return condition with visual feedback was not different from the adaptation obtained in regular adaptation with visual feedback (condition ON), consistent with findings from a fast-paced adaptation protocol (Gray et al. 2014). Thus the fast return protocol allows sufficient time to complete visual error estimation and any associated learning process for amplitude adaptation. The reason for the lack of adaptation in condition OFR must hence be the lack of reliable proprioceptive eye position signals during the short dwell time at the saccade landing location.

The design of our study contains two implicit assumptions about the nature of the proprioceptive eye position signal. First, the signal's sensitivity has to be smaller than 2° to be able to detect the change in amplitude after the first adaptation phase. Second, the proprioceptive signal has to remain unchanged during the first adaptation phase. If one of these assumptions were incorrect, the proprioceptive signal should not serve as a learning signal in our experiment. Since we found the expected differences in adaptation during the second adaptation phase, these assumptions can be considered to be applicable. Hence our results show that the proprioceptive signal does not fully adapt during the primary adaptation phase. It may be that adaptation of the proprioceptive signal is not possible or takes place on a slower time course.

In a previous study, Seeberger et al. (2002) investigated the use of nonvisual eye position information on saccadic adaptation in the macaque monkey, using a similar protocol of initial adaptation and secondary (de)adaptation with and without visual feedback. Our results in conditions ON and OF resemble the findings of that study. Both Seeberger et al. (2002) and our study found reduced secondary adaptation in trials without postsaccadic visual feedback compared with trials with postsaccadic visual feedback. As Seeberger et al. (2002) saw no difference between the condition without visual feedback and a condition in which the monkey simply remained in darkness for 20 min, they concluded that nonvisual information cannot drive saccadic adaptation. However, the monkeys were allowed to make saccades during the control condition in darkness and hence might have experienced proprioceptive feedback signals during that time. In our control condition FI, participants had to fixate such that no saccades of size comparable to the adapted saccade were conducted and no error signals could emerge. Moreover, Seeberger et al. (2002) did not include the fast return condition, which is the critical condition in our design. Also, adaptation mechanisms in monkeys and humans are known to differ in some respects (Albano and King 1989; Deubel 1987; Frens and van Opstal 1994; Straube et al. 1997; Watanabe et al. 2003), such that any differences between our results and those of Seeberger et al. (2002) might also be related to species differences.

Strictly speaking, the presentation of the fixation point after the saccade in the fast return protocol might have served as an 11° error signal in the backward direction. However, if such an error would be used as a learning signal for amplitude modification, then the saccades in condition OFR should become shorter over time. This was not the case in our study (compare Fig. 2). Furthermore, different studies on how visual errors drive motor adaptation showed that a visual error that matches the size of the initiated saccade usually does not lead to significant adaptation (Robinson et al. 2003; Wei and Körding 2009).

A contribution of proprioceptive eye position signals to postsaccadic error estimation might help to explain a common finding of studies that used a protocol of constant error adaptation. In this protocol, the in-flight measurements of gaze position are used to calculate the saccade landing position. Then the target is stepped to a new location during the saccade so that it always appears at a constant distance from the landing position (Robinson et al. 2003; Zimmermann and Lappe 2010). In this case, the same postsaccadic error is constantly maintained and should induce continuous changes in saccadic amplitude. Yet, amplitude in this paradigm progresses toward an asymptotic level. If adaptation was based solely on a visual error signal, amplitude changes should not stop as long as the error persists. However, if proprioceptive eye position information is included in the error estimation, it could signal an accurate movement. A discrepancy between visual and proprioceptive error estimates could influence error attribution (Chen-Harris et al. 2008; Ethier et al. 2008; Kording et al. 2007) and hence modify adaptation.

We conclude that saccadic adaptation uses proprioceptive eye position after the saccade to monitor the success of the eye movement and to calculate any required amplitude modification based on the comparison of the expected and the experienced postsaccadic eye position. The multimodal combination of visual and proprioceptive error likely increases the stability and consistency of the adaptation process, explains limited learning in the constant error adaptation, and may help to keep vision and action control in register.

GRANTS

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.G. and M.L. conceived and designed research; S.G. performed experiments; S.G. analyzed data; S.G. and M.L. interpreted results of experiments; S.G. prepared figures; S.G. drafted manuscript; M.L. edited and revised manuscript; S.G. and M.L. approved final version of manuscript.

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