

# The Influence of the Consistency of Postsaccadic Visual Errors on Saccadic Adaptation

Katharina Havermann and Markus Lappe

*Psychologisches Institut II and Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, Westfälische Wilhelms-Universität Münster, Münster, Germany*

Submitted 3 November 2009; accepted in final form 8 April 2010

**Havermann K, Lappe M.** The influence of the consistency of postsaccadic visual errors on saccadic adaptation. *J Neurophysiol* 103: 3302–3310, 2010. First published April 14, 2010; doi:10.1152/jn.00970.2009. The saccadic system is a prime example of motor control without continuous visual feedback. These systems suffer from a strong vulnerability against disturbances. The mechanism of saccadic adaptation allows adjustment of saccades to alterations arising not only from anatomical changes but also from external changes. The weighting of errors according to their reliability provides a strong benefit for an optimized control system. Thus the consistency of visual error should influence the characteristics of adaptation. In the typical adaptation paradigm a visual error is introduced by stepping the target during the saccade by a given amount. In this paradigm, the retinal error varies with the accuracy of the saccade and the step size. To study the influence of error consistency we use a variant of the adaptation paradigm which allows to specify a constant error size. Intrasaccadic target step sizes were calculated with respect to the predicted landing position of each individual saccade. The consistency of the visual error was varied by introducing different levels of noise to the intrasaccadic target step. Different mean intrasaccadic target step sizes were examined: positive target step, negative target step, and a condition in which the mean of the error distribution was clamped to the fovea. In all three conditions saccadic adaptation was strongest when the error was consistent and became weaker as the error became more variable. These results show that saccadic adaptation takes not only the average error but also the consistency of the error into account.

## INTRODUCTION

The question of how the CNS controls fast movements when online feedback is unavailable is important for the understanding of motor control. Saccades are the fastest movements humans perform and provide a prime example of movements without online visual feedback. The mechanisms of motor control can be analyzed by the paradigm of saccadic adaptation. In saccadic adaptation, the subjects are asked to make a saccade to a suddenly appearing target. An artificial error is introduced by displacing the target while the subject is making the saccade. When this error occurs repeatedly over time a modification of the saccadic amplitude toward compensation of the error takes place. The postsaccadic visual error is an important driving signal for saccadic adaptation (Noto and Robinson 2001; Wallman and Fuchs 1998). Performance of a corrective saccade or signals from the muscle afferents are not crucial (Lewis et al. 2001). Thus computational models that include the visual feedback as teacher for saccadic adaptation use the postsaccadic retinal error as a learning signal (e.g.,

Chen-Harris et al. 2008; Dean et al. 1994; Gancarz and Grossberg 1999; Harris and Wolpert 2006). The standard paradigm for saccadic adaptation, the McLaughlin paradigm (McLaughlin 1967), controls the displacement of the saccade target. However, the target displacement is equal to the visual error only in the case of a perfect saccade. Saccadic inaccuracy generates variability in the visual error, which adds to any artificially induced error. To receive reliable information about the effect of consistency of the visual error on saccadic adaptation it is thus necessary to directly vary the retinal postsaccadic visual error. We do this by controlling the error relative to the landing point of each individual saccade.

The principle of optimality of the control process offers a valuable theoretical perspective on motor control. For instance, Kording and Wolpert (2004) applied the principle of Bayesian integration to online corrections of hand movements. In this study, visual information about a virtual error of the hand position was blurred to different extents. With decreasing reliability of visual information the subjects tended to rely more on their proprioception as the prior. In the field of saccadic adaptation different optimality criteria have been considered. In the open loop model of Harris and Wolpert (2006), accuracy and speed are combined in an optimal manner in the main sequence. Recent closed loop models combine the adaptation of a forward model and a representation of the target in an optimal way, to reproduce the velocity profile of adapted saccades (Ethier et al. 2008). In the present study we propose that the consistency of the error information plays a role in determining the reliability of the feedback and in optimizing adaptation. We therefore expect less consistent errors to be less reliable and, on average, to lead to weaker saccadic adaptation than errors that are more consistent, independent of the absolute average size of the error. In the present study the interplay of visual errors of different consistencies is examined by measuring the averaged gain change. We apply intrasaccadic target steps of different variability and study the influence of the consistency for inward and outward adaptation. Furthermore, to closely examine the behavior of small errors, which resemble the majority of errors in a natural situation, we include a condition (termed “foveal step condition”) in which the target stepped directly onto the landing position and thus induced, on average, zero retinal error. Together with inward and outward adaptation the general dependence of saccadic adaptation on visual consistency is determined.

## METHODS

The adaptation procedure followed a modified McLaughlin paradigm (McLaughlin 1967; Robinson et al. 2003). In this paradigm a

Address for reprint requests and other correspondence: K. Havermann, Psychologisches Institut II, Fliehdnerstr. 21, 48149 Münster, Germany (E-mail: k.havermann@uni-muenster.de).

target appears while the subject looks at a fixation point. During the subject's saccade to the target, a displacement of the target is introduced that results in a postsaccadic visual error. Over the course of many consistent trials the metrics of the saccade adapt and the saccadic amplitude changes in the direction of the displacement. To control the influence of the postsaccadic visual error, we calculated the intended displacement with respect to the predicted landing point of the saccade. Therefore the induced error is equal to the retinal error. In the following, we will refer to this postsaccadic retinal error as the visual error.

### *Stimuli and recording setup*

The subject was placed at a 40 cm distance from a 22-in. monitor (Eizo FlexScan F930). This resulted in visual field of  $40^\circ \times 30^\circ$ . To avoid visual references the room was completely dark. A transparent foil reduced the luminance of the monitor by 2 log units and prevented the visibility of the monitor borders. All stimuli were presented with a refresh rate of 120 Hz and a resolution of  $600 \times 800$  pixels. The stimuli were red circles of a diameter of  $1^\circ$  and a luminance of  $0.06 \text{ cd/m}^2$ . Eye movements were recorded with the EyeLink 1000 system (SR Research Ltd., Mississauga, Ontario, Canada). The head was sustained with a chin rest. All measurements were taken at 1,000 Hz. For all subjects the left eye was recorded. Viewing was binocular.

### *Experimental procedure*

The fixation point was presented centrally with respect to the vertical axis of the field of view. The vertical position was randomized in the central third of the monitor, which equaled an area of  $10^\circ$  of visual angle. This variation in eye position was introduced to avoid stereotypic response behavior. The horizontal position of the fixation point remained constant throughout all the experiments. After fixation was established by the detection of a stable eye position in an area of  $3^\circ \times 3^\circ$  around the fixation point a target appeared  $15^\circ$  to the right of the fixation point. The subject was instructed to saccade to the target as soon as possible. When the eye velocity exceeded  $9.6^\circ/\text{s}$  the target was extinguished. The target reappeared immediately after the saccade at a predetermined position relative to the saccade landing position. It remained there for 1 s plus a variable delay of 100 ms to avoid stereotypy. To determine the position of the reappeared target T2 the landing point of the saccade was calculated during the experiment. The direction of gaze was monitored online and eye velocity was calculated from the differential quotient of the last four data points. As soon as this velocity measure fell to  $<30^\circ/\text{s}$  the last data point measured was defined as endpoint of the saccade. In the later off-line analysis of saccade behavior, eye movement events detected by the EyeLink software were used. These involved a  $22^\circ$  velocity threshold and a  $4,000^\circ/\text{s}^2$  acceleration criterion. A comparison between these two measures of final eye position revealed a median prediction accuracy of  $-0.06^\circ$  with quartiles of  $0^\circ$  and  $-0.17^\circ$ . The temporal delay after detection of the velocity criterion and the presentation of the target fell below 20 ms, or two monitor refreshes. The online calculation of the landing position revealed a systematic deviation from the EyeLink criterion for two subjects attributed to a dynamic overshoot. Their data were included in the analysis because their results did not differ from those of the other subjects. The offline analysis was unaffected by the dynamic overshoot.

Every trial started with a drift correction at the position of the fixation point. The subject fixated a calibration target and pressed the space button of the keyboard. The eye position at the time of button press was then used as the coordinate origin for the following trial. Trials in which the saccade started earlier than 110 ms after target appearance and trials in which the saccade duration was less than 20 or more than 80 ms (indicating a saccade of highly inappropriate amplitude) were excluded from further analysis.

### *Design of adaptation session*

Every adaptation session consisted of three types of trials. In the first 10 trials the target was extinguished while the subject performed the saccade. Thus no visual feedback was given after the saccade. These trials were called target off trials and were performed to introduce the subject to the situation without feedback. After target-off trials the target reappeared not until the start of the next trial, when the fixation point was shown. In the next 10 trials, called no-step trials, the target reappeared at the original position. These trials were conducted to prevent a strong undershoot at the start of the subsequent adaptation session, since, as will be shown later, some subjects reacted with an increased undershoot in target off trials. After these 20 initial trials, 300 adaptation trials were performed. In the adaptation trials the target was displaced in a predetermined way to vary the consistency of visual feedback. After each session, 50 deadadaptation trials were performed. Successive sessions with the same subject were separated by at least 24 h. The mean duration between successive sessions was 5.5 days. The order of sessions was counterbalanced to avoid order effects. Different error sizes and consistencies were run in different adaptation sessions (see following text). One particular condition involved foveal-step trials in which the target was stepped onto the landing position of the saccade such that no retinal error occurred. Altogether, 3,280 trials were recorded for each subject.

### *Consistency and mean target step conditions*

Our main interest was in the role of the visual error consistency. Therefore the main factor of the experiment was the variance of the visual error. For each trial, the intended error was drawn pseudorandomly from a Gaussian distribution with a predetermined SD that described the visual error consistency. The visual error consistency was varied with three different strengths:  $0^\circ$  (high consistency condition),  $2^\circ$  (medium consistency condition), and  $4^\circ$  SD (low consistency condition). The second factor of the experiment was the average target step size, which is the average distance between the landing point and the location of presentation of the postsaccadic target. Target steps of  $-3^\circ$  (negative step),  $0^\circ$  (foveal step), and  $3^\circ$  (positive step) were tested. Therefore, for each subject nine adaptation sessions were recorded. Figure 1 visualizes the distribution of visual error for the three mean target step conditions in nine histogram plots. From left to right the consistency decreases; from top to bottom the target step size increases.

In addition to the nine adaptation conditions shown in Fig. 1 two comparison conditions were measured in which exclusively target-off and no-step target trials were presented. They were restricted to 200 trials because they involved no strong gain change. These two conditions were compared to examine the role of the existence of visual feedback signals (i.e., postsaccadic target information) in saccadic stability.

### *Data analysis*

In our adaptation paradigm the mean retinal error remained constant throughout the whole adaptation session and the gain change often did not saturate within 300 trials. In the absence of saturation it seemed inappropriate to determine an absolute gain change as a measure of the amount of adaptation or to use an exponential function to model the data, even though saccadic adaptation even in the constant error paradigm is known to show an exponential time course (Robinson et al. 2003). Instead, as a reasonable approximation of a slowly saturating exponential function, we calculated a linear regression on the amplitude data and used the slope of the linear fit as a measure for the average rate of gain change during the session. This allowed us to include all data from the session in our estimate of the amount of adaptation, thus giving a more stable estimate than a simple difference analysis based on a limited number of pre- and postadap-

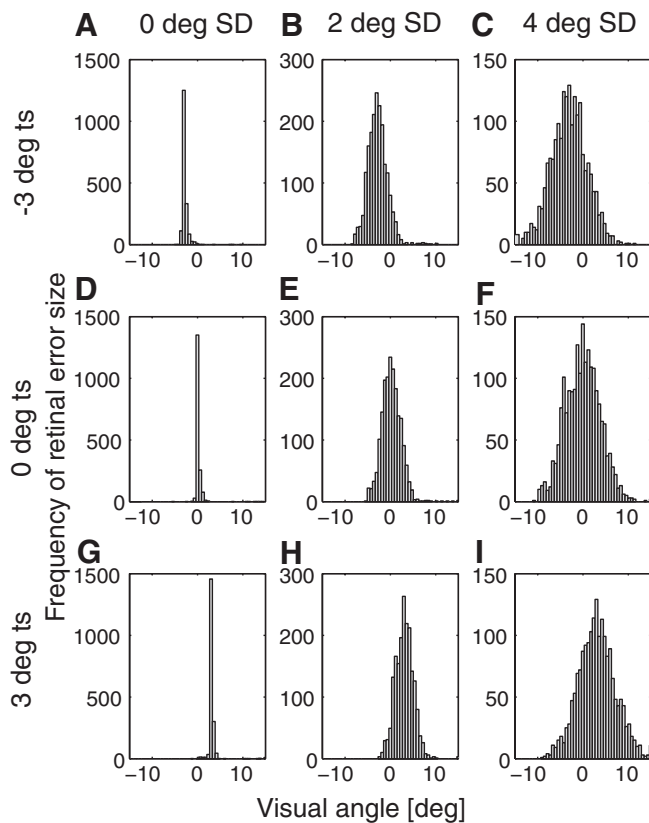


FIG. 1. Histogram of retinal errors for the different inconsistent conditions of all subjects. Bin size:  $0.6^\circ$ . From left to right: decreasing consistency (high [A, D, G], medium [B, E, H], low [C, F, I]). From top to bottom: negative target step (A, B, C), foveal step (D, E, F), and positive target step (G, H, I).

adaptation measurements. However, this method may slightly underestimate the adaptation because the difference between the pretrials and the first few adaptation trials is not taken into account because the pretrials are not included in the linear fit. Indeed, in some conditions significant adaptation already took place between the last five pretrials and the first five adaptation trials. This was in the inward high consistency condition [ $t(6) = 2.65$ ,  $P = 0.038$ ] and the inward low consistency condition [ $t(6) = 3.90$ ,  $P = 0.008$ ]. A rapid drop of saccade amplitudes for inward adaptation is also known from the McLaughlin paradigm (Hopp and Fuchs 2004), but it might even be stronger in our constant retinal error method. Nonetheless, because this could lead only to an underestimation of the gain change, our linear fit is a conservative measure of gain change. In an additional analysis we confirmed that the main results were consistently obtained in a classical analysis of the differences between the preadaptation trials and the last 20 adaptation trials. The correlation between the data from the two types of analysis was 0.95. We prefer to report the values of the linear regression slope since the exact values for the gain change in the pre-post analysis depend somewhat on the choice of pretrials and posttrials, respectively. Therefore the linear fit was chosen as most reliable analysis tool. Thus in the following the unit of the gain change rate averaged over a whole session will be [deg/trial]. The preadaptation gains for the seven subjects were close to unity (0.88, 0.94, 0.90, 0.82, 0.73, 0.98, 0.99).

### Subjects

The experiment was conducted with nine subjects. Two of the subjects had to be excluded from the data analysis because their trial exclusion rate was exceeding 30%. Thus, data from seven subjects (one author, two male, one left-handed, mean age 26.2 yr) will be presented.

## RESULTS

We investigated the influence of the consistency of the visual error on the rate of saccadic adaptation. First, we analyzed the influence of consistency of the visual error on adaptation rate for inward and outward adaptation. Second, we examined saccade behavior in the foveal condition and compared its results to those of the inward and outward case. Figure 2 shows data from one subject in all conditions. The dots show the saccadic landing positions; the crosses show the positions of the reappearing target. In the first row contains the negative target step conditions, the second row the foveal conditions, and the third row the positive target step conditions. From left to right the consistency is decreasing, which is clearly visible in the increased scattering of the positions of the reappearing target. Inward and outward adaptation can be seen in the high consistency condition on the right for negative and positive target steps, respectively. Moreover, this subject showed a pronounced drop of saccadic amplitude in the first few adaptation trials of Fig. 2, A and G. This drop was much weaker in the other conditions and generally in most other subjects. The amount of adaptation clearly differs between the different consistency conditions. The following sections will analyze the different conditions for the whole group of subjects.

### Negative target step

The negative step condition consisted of an average visual error of  $-3^\circ$  with three consistency values: high ( $0^\circ$  SD), medium ( $2^\circ$  SD), and low ( $4^\circ$  SD). Inward adaptation occurred in all three cases. Therefore, the adaptation rate was negative. A comparison of the different consistency conditions for neg-

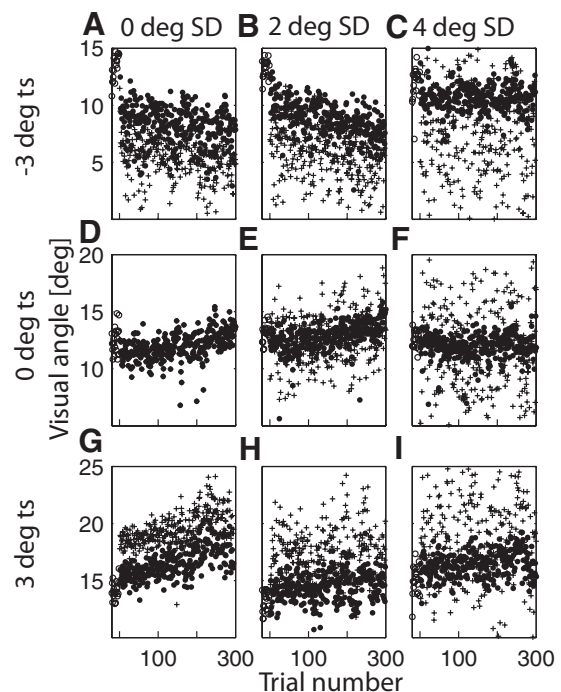


FIG. 2. Saccadic endpoints (dots) and target reappearance positions T2 (crosses) for one subject in all adaptation sessions. Pretrials are shown as circles. From left to right: decreasing consistency (high [A, D, G], medium [B, E, H], low [C, F, I]). From top to bottom: negative target step (A, B, C), foveal step (D, E, F), and positive target step (G, H, I).

ative target steps showed that the adaptation rate decreased with decreasing consistency. In the high consistency condition the average gain change rate was  $-0.0131$  deg/trial. For medium consistency the gain change rate decreased to  $-0.0098$  deg/trial and, in the low consistency, to  $-0.0065$  deg/trial. A repeated measures ANOVA revealed a significant attenuation effect [ $F(2,6) = 9.25, P = 0.004$ ]. Figure 3A shows the average gain change rate over all subjects. The consistency is decreasing from left to right. In a Bonferroni corrected  $t$ -test the difference between the high consistency and the low consistency conditions was significant [ $t(6) = 6.48, P = 0.002$ ].

#### Positive target step

The positive step condition involved the three consistency conditions with an average visual error of  $+3^\circ$ . Figure 3B shows the results. In the high consistency condition outward adaptation occurred with an average rate of  $0.0042$  deg/trial. In the medium consistency condition the outward gain change rate was virtually zero ( $0.0015$  deg/trial). In the low consistency condition the adaptation direction was reversed and an average gain decrease occurred ( $-0.0022$  deg/trial). In a repeated measures ANOVA the difference between the consistency conditions was significant [ $F(2,6) = 7.39, P = 0.008$ ]. The large between-subject variability in the positive target step data compared with the negative or foveal step data turned out to result from the behavior of a single subject. That subject showed outward adaptation in the high consistency condition, but reversed gain change in the medium and low consistency conditions. In a Bonferroni corrected  $t$ -test the difference between the high consistency and the low consistency condition was significant [ $t(6) = 6.22, P = 0.002$ ].

The reversal of the adaptation direction in the low consistency condition might be related to an overall tendency to reduce saccadic amplitude over a large number of saccade trials. To check whether this was the case, we examined the development of the saccade amplitude in two comparison conditions: the target-off and the no-step condition. Both conditions gave a slight decline of saccade amplitude over the course of the sessions (Fig. 5C). The rate of gain change was negative in both cases. No significant differences were found between the two conditions [ $t$ -test,  $t(6) = 1.30, P = 0.24$ ]. As indicated by the error bars, however, large differences occurred between subjects and between conditions within individual subjects.

The initial observation of a reversal of adaptation direction in the low consistency positive error condition can therefore be

related to the gain change rate of the two comparison conditions. The inversion of the gain change rate can be considered as the superposition of the induced adaptation and a decrease of saccadic amplitude over a large number of trials (possibly a fatigue effect) that occurs independently of the postsaccadic error signal. In combination with the attenuation of outward adaptation that results from the decrease in error consistency a net gain decrease occurs. If the gain change rate of the target-off comparison condition, shown in Fig. 5C, is considered as a baseline, no inward adaptation occurs in the positive target step conditions. The net gain changes after subtracting the gain change rate of the target-off condition are depicted in Fig. 3C for both the negative (neg ts) and positive target step (pos ts) condition. They are of comparable size. For both conditions attenuation is clearly visible.

#### Foveal step

The saccadic system is used to deal with small errors in the saccade amplitude. The typical hypometry of saccades of large amplitudes already induces a systematic visual error. Normally, this undershoot is not compensated. Large amplitude saccades remain hypometric even after a large number of trials. It is still an open issue why the hypometry is not compensated and how this lack of compensation relates to saccadic adaptation. One possibility is that the saccadic system maintains an intended undershoot of large saccades and that saccadic adaptation steers the saccade amplitude to achieve this undershoot. This could be achieved by shifting the set point of the error to the intended undershoot amplitude.

The foveal step condition provides a way to test this hypothesis. In the foveal step condition, the postsaccadic target was on average presented at the landing position of the eye. Therefore no net retinal error occurred. In the high consistency foveal step condition the median accuracy of the calculation of the landing position was  $-0.025^\circ$ , with quartiles of  $-0.125$  and  $0^\circ$ . An active maintenance of a systematic undershoot should then result in an inward gain change and reduce saccade amplitude. The average gain change rates for the three consistency conditions were indeed slightly negative ( $-0.0045$  deg/trial for the high consistency condition,  $-0.0041$  deg/trial for the medium consistency condition, and  $-0.0065$  deg/trial for the low consistency condition). However, the amount of the gain change rate did not exceed the gain change rate of the comparison conditions in which the target stayed at the initial position (no-step) or in which the target was extinguished altogether (target-off). Moreover, the rate of gain change varied strongly

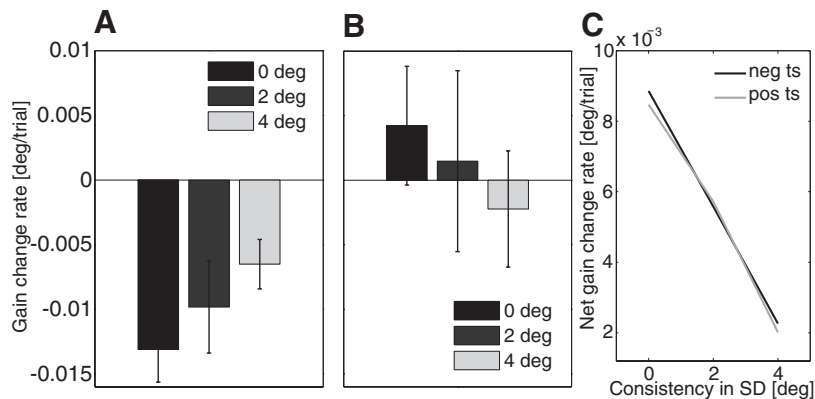


FIG. 3. Average gain change for the positive (A) and the negative (B) target steps in the 3 consistency conditions. The error bars show the SDs. C: net gain change in the 3 consistency conditions after subtracting the gain change rate of the target-off comparison condition (Fig. 5C). The net gain change rate is attenuated for both, negative (neg ts) and positive target steps (pos ts).

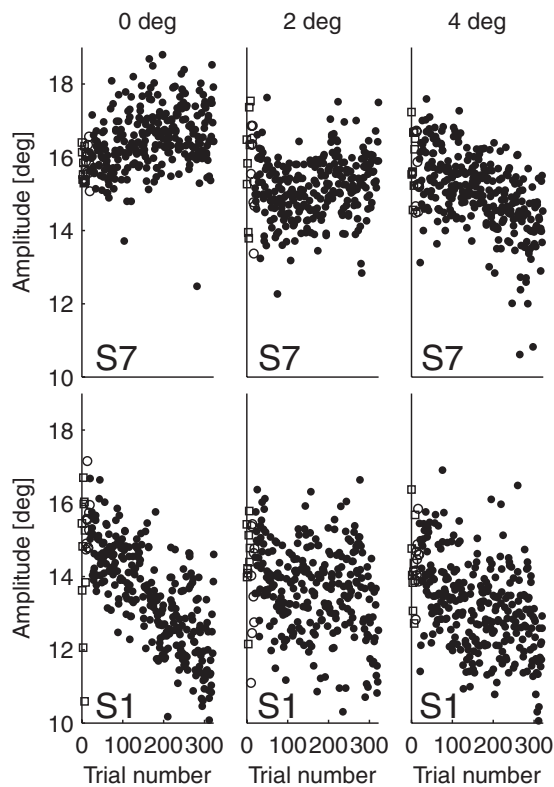


FIG. 4. Development of saccadic adaptation in the foveal step conditions for two example subjects. Shape code type of trial: square: target-off; circle: no-step; dot: adapt trials. Subject S7 develops a gain increase, whereas subject S1 shows a gain decrease. Both behaviors disappear with decreasing consistency.

between subjects. Three out of seven subjects showed outward adaptation and four showed inward adaptation in the high consistency foveal step condition. We therefore divided the subjects in an inward group and an outward group. Figure 4 shows the adaptation curves for the three foveal conditions for two representative subjects showing opposite gain change rates, an amplitude increase for subject S7, and an amplitude decrease for subject S1. Figure 5 shows the dependence of the gain change on error consistency for the group of subjects that showed inward adaptation (Fig. 5A) and the group of subjects that showed outward adaptation (Fig. 5B). In both groups the rate of gain change decreased with decreasing consistency. As

in the positive step conditions, the subjects that exhibited outward adaptation in the foveal step condition showed an inversion of the gain change in the low consistency condition that is likely due to a general inward tendency. To determine the dependence of the rate of gain change on the error consistency over all subjects we inverted the sign of the gain change values of the outward adapting subjects. A repeated measures ANOVA over all subjects showed a significant attenuation of the adaptation rate with decreasing consistency [ $F(2,6) = 4.56$ ,  $P = 0.034$ ]. In Fig. 5D the net gain changes for the inward and outward groups are depicted in the same manner as that in Fig. 3C. The net gain change is attenuated with decreasing consistency.

We wondered whether the direction of gain change was related to the initial hypo- or hypermetry of the subject. A correlation may be expected if subjects actively maintain an individual bias to under- or overshoot (Henson 1979). Our data do not unambiguously support such an active maintenance explanation, however. Figure 6 shows a scatterplot of initial gain and gain change for all seven subjects. The Pearson correlation coefficient between initial gain and gain change was only 0.53. One subject showed a behavior completely opposite to the prediction. Although the subject showed initial hypometry the gain change rate was positive.

#### Interaction between mean visual error and consistency of visual error

Since the group analysis in the foveal condition revealed an attenuation comparable to that in the positive and negative error conditions we wanted to further analyze the dependence of the attenuation on the mean and the variance of the error. Thus all data were combined in a two factor repeated measures ANOVA with mean visual error and consistency of visual error as main factors. If a decreased consistency attenuates gain change an interaction of the two factors should arise. The influence of the mean target step was significant [ $F(2,6) = 16.6$ ,  $P = 0.0003$ ]. The influence of consistency did not reach significance [ $F(2,6) = 0.67$ ,  $P = 0.53$ ]. The interaction between the mean and consistency was again significant [ $F(4,6) = 6.8$ ,  $P = 0.0008$ ]. In a second step both the main target step and an interaction term of the two factors mean target step and consistency were included in a multilinear regression analysis. For this analysis, we computed the actual

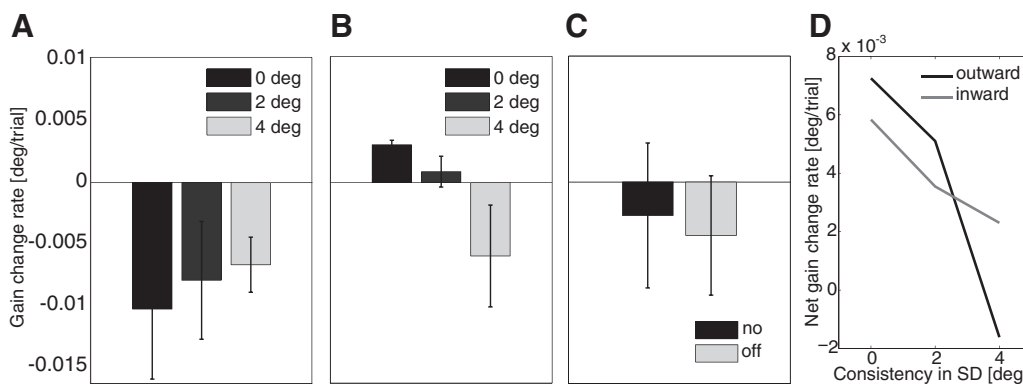


FIG. 5. Average gain changes in the foveal step condition for the groups of inward adapting subjects (A) and outward adapting subjects (B). The error bars show the SDs. C: average gain changes in the 2 comparison conditions consisting of no-step and target-off trials. D: net gain change in the 3 consistency conditions after subtracting the gain change rate of the target-off comparison condition (Fig. 5C). The net gain change rate is attenuated for both negative (neg ts) and positive target steps (pos ts).

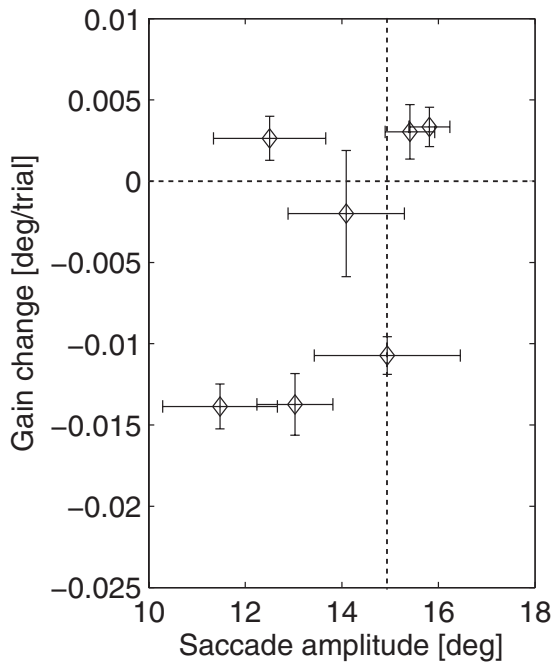


FIG. 6. Correlation between initial hypo-/hypermetry and gain change. On the x-axis the initial saccade amplitude and on the y-axis the gain change in deg/trial is shown.

values of mean target step and consistency over all valid trials of each session. They differ from the theoretical values because of trials that had to be removed from data analysis as described earlier. In Fig. 7 the gain change rates for all subjects and conditions are shown as a scatterplot. A view from the consistency axis is depicted. The plane indicates the result of the multilinear regression. Dark lines indicate the original mean target step and consistency conditions. In the direction of decreasing consistency the slope is flattening. The  $R^2$  is 0.51, due to the great intersubject differences.

*Trial-by-trial analysis*

For saccadic adaptation to occur a trial-by-trial influence of the postsaccadic error on the subsequent saccade is necessary. As the visual error induces changes in the amplitude of saccades, any error ought to have an effect on subsequent saccadic amplitudes. The observed attenuation of saccadic adaptation in the low consistency condition intuitively contradicts the importance of the trial-by-trial influence of the visual error

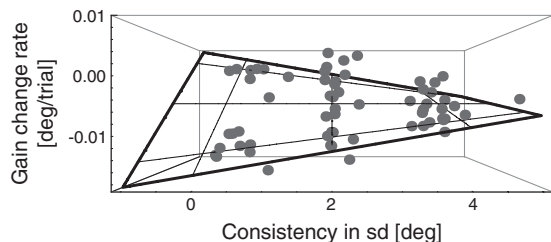


FIG. 7. Planar fit of the gain change data from the multilinear regression. Dark lines indicate the original conditions of consistency and mean target step; x-axis: consistency, y-axis: mean target step, z-axis: gain change rate. For the high consistency condition on the left, a clear difference in the gain change rate is visible comparing different mean target steps from front to back. From left to right the gain change rate becomes more comparable for all mean target step conditions.

because, in addition to the error of the current trial, its consistency with the errors of preceding trials is also important. We carried out a correlation analysis to show that even in the attenuated case of low consistency a trial-by-trial effect takes place. In this analysis, we correlated the amplitude of trial  $n + x$  with the visual error in trial  $n$ . We chose the amplitude rather than the amplitude change because it is less noisy and gives more robust results. This is a valid approach because the visual errors are equally distributed over time. A general trend in the data, as revealed by the gain change rate, thus does not contribute to the correlation. For instance, in the positive target step conditions a positive correlation means a large error is likely followed by a large amplitude.

For the six medium and low consistency conditions Fig. 8 shows the correlation strength between the visual error and the amplitude for different temporal offsets between the error and the saccade. The x-axis shows the difference in trial number  $\Delta(\text{trial}_{\text{saccade}}, \text{trial}_{\text{error}})$ . Because of the great number of comparisons, 99% confidence intervals were determined for the correlations received. This was accomplished by bootstrapping the data with a bootstrap sample size of 1,000. The filled symbols show data significantly different from zero. A clear increase in correlation is visible for the saccadic amplitude directly following the error trial  $[\Delta(\text{trial}_{\text{saccade}}, \text{trial}_{\text{error}})]$ . Five of six correlations in this time step difference in addition to one for the following time step are significant. Thus a trial-by-trial influence exists even in the low consistency conditions. Yet, the average correlation is small, never exceeding 0.13. The correlations are higher in the low consistency than those in the medium consistency conditions, probably because the smaller scales of visual error in the medium consistency condition are more sensitive to measurement errors. Yet, this analysis makes clear that, regardless of the influence of consistency, every trial provides a contribution to the adaptation.

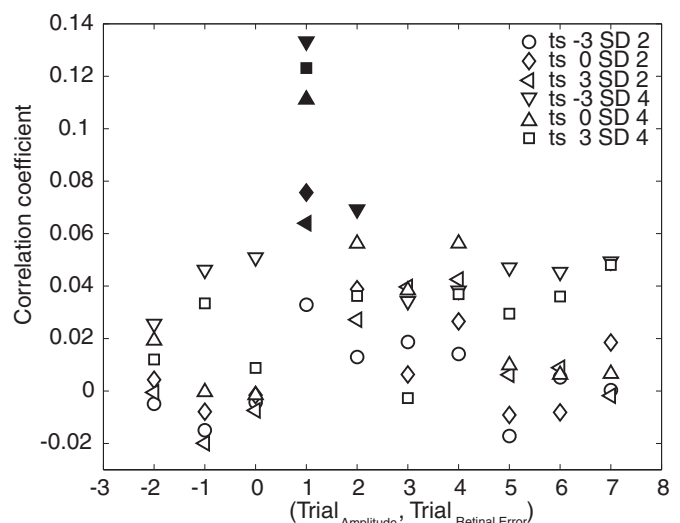


FIG. 8. Correlation coefficients between the saccadic amplitude and the visual retinal error as a function of the difference in trial number between the two. An increase in correlation is clearly visible for the amplitude of the trial immediately following the error  $\Delta(\text{trial}_{\text{saccade}}, \text{trial}_{\text{error}}) = 1$ . The line styles refer to the target step ts and consistency conditions (given in SD). Significant results are shown as filled symbols.

## DISCUSSION

Our study revealed a clear dependence of the saccadic gain on visual error consistency. The effect of consistency was tested for three different mean target steps: positive, negative, and zero foveal step and for three levels of consistency: high, medium, and low. In the high consistency negative target step condition inward adaptation occurred. In the high consistency positive target step condition outward adaptation was observed. In the foveal step condition both directions of gain change were found. For all mean target step conditions the rate of gain change was largest in the high consistency conditions and decreased with reduced consistency. A correlation analysis revealed a trial-by-trial influence of the visual error on the saccade amplitude, also for the low consistency conditions.

From the perspective of optimal control the observed dependence of the gain change rate on error consistency appears to be very sensible. It would fit with a Bayesian approach to motor learning in which the distribution of visual errors serves to form an expectation of future errors and of the reliability of that expectation as realized in Wei and Kording (2009). Our results could thus be interpreted as a weighting of visual errors with respect to an expected range of errors. A similar framework was proposed by Burge et al. (2008) for hand movements. In that study, an optimally adaptive control was realized via a Kalman filter approach. The behavior of this adaptive control model also showed attenuation with decreased consistency.

A different interpretation for the attenuation involves the possible occurrence of conflicting error signals within a single adaptation session. When the intertrial variance of target steps is large, as in the low consistency conditions, some trials of a particular adaptation direction might impose a visual error that is in the opposite adaptation direction. For example, if the mean error is  $-3^\circ$  and the SD of the error distribution is  $4^\circ$ , most of the retinal errors are falling on the left side of the fovea. However, 23% of the errors fall right from the fovea, simply because of the width of the error distribution. But in fact, with respect to T1 the average number of all positive target steps in the negative target step low consistency condition was 8 of 300 trials per session. In the medium consistency condition, however, with respect to T1 that number was virtually zero, such that oppositely directed visual errors almost never occurred. Thus conflicting error signals cannot sufficiently explain the dependence of the rate of gain change on error consistency. Occasionally, targets may reappear even on the opposite site of the fixation point (FP). However, this occurred in less than 0.5% of trials (1.6% in the low consistency conditions).

Our analysis of the two comparison conditions revealed no clear difference in gain change rate between no-step trials in which the target remained at its original position and target-off trials in which the target disappeared during the saccade. In both conditions the saccadic amplitude decreased somewhat over time. This decrease might arise from fatigue in the eye muscles or in the control structures that is not compensated (Barash et al. 1999). However, although this general decrease was observable in the average, on the single subject level more diverse behaviors occurred. Two of the seven subjects showed a gain increase over time in the no-step condition, possibly reflecting a decrease of saccadic hypometria via adaptation.

Two other subjects showed a gain increase over time in the target-off condition. Bonnetblanc and Baraduc (2007) described a similar increase in saccadic gain when the saccade target was extinguished during the saccade. They suggest that saccade amplitudes adapt in this condition because the target-off condition does not allow for corrective eye movements. They argue that undershoot is an optimal strategy only when corrective eye movements are possible.

Although two subjects exhibited an increase in saccade amplitude in the no-step trials, the majority of our subjects remained hypometric even after many trials of the no-step condition. This is in accord with the general agreement that saccadic undershoot observable in saccades with larger amplitudes is usually not compensated by adaptation. In many computational models the undershoot is therefore not considered, but is filtered out before providing the error signal to any motor parameter regulating system. The simplest way to do this is a shift of the retinal error by the amount of intended undershoot. The high consistency foveal step condition contained only very small visual errors. This allowed us to examine the treatment of small errors in detail. According to the preceding argument, the zero retinal error that is induced on average in the foveal step condition should lead to inward adaptation. This did not occur. Instead, three of the seven subjects exhibited outward adaptation in the foveal step condition. Yet, the strength of this outward adaptation depended on error consistency and decreased when errors became inconsistent.

Inward adaptation is typically faster than outward adaptation (Deubel et al. 1986; Noto et al. 1999; Panouilleres et al. 2009; Robinson et al. 2003). Therefore, the influence of noise should be different for inward and outward adaptation. If the two mechanisms would combine linearly on a trial-by-trial basis then inward adaptation should overcome outward adaptation in the low consistency foveal-step condition. This was not the case.

We have used the postsaccadic visual error with respect to the landing position of the eye for our analysis because this retinal error is considered the driving force behind saccadic adaptation (Noto and Robinson 2001; Wallman and Fuchs 1998). Alternatively, the system might use the target step as error signal if an efference copy of the motor command is accurate enough to estimate the landing point in relation to the target location (Collins et al. 2009). This would in general allow the saccadic system to determine the absolute saccadic error regardless of the retinal error. The foveal-step condition provides a test of this possibility. As the saccades were in general hypometric, in the foveal condition, the target was effectively always displaced inward. Therefore inward adaptation should result in this condition if the target step itself is used for the adaptation. This was not the case. However, our main finding that the rate of adaptation depends on the consistency of the error signal remains true even if the error is calculated with respect to the initial target location rather than with respect to the landing point of the eye.

Srimal et al. (2008) studied saccadic adaptation on a trial-by-trial basis. They found learning rates of comparable size for classical saccadic adaptation and for a random step paradigm. Note that Srimal et al. (2008) used the same unit [deg/trial] on a trial-by-trial basis, which is different from ours, because in our averaged measure learning rates in opposite directions

compensate each other. We quantified an effective gain change rate to more closely determine the magnitude of learning in dependence of the error size. While we varied the consistency in the different conditions, we balanced retinal errors in every session. This is why we can exclude the possibility that a linear weighting of errors by a single one-timescale adaptation mechanism can account for the data, although trial-by-trial learning existed for all consistency conditions. In a purely linear adaptation mechanism no difference in gain change should appear for the three consistency conditions because the mean error is the same in all three conditions. A nonlinear weighting, however, could explain the observed dependence on error consistency. Indeed, experimental data in the monkey (Robinson et al. 2003) revealed a nonlinear gain change pattern in response to different retinal errors. The strongest response occurred for a 3° target jump. Since our study also used a 3° target jump the high consistency condition may have induced optimal adaptation behavior, whereas the lower consistency conditions may have induced less adaptation because many retinal errors were different from the 3° optimum. The Bayesian approach of Wei and Kording (2009) also suggested that a nonlinear weighting of errors may underlie saccadic adaptation. For small errors a linear dependence can be assumed, whereas for greater errors the gain change per trial is saturating.

The dependence of adaptation rate on error consistency supports the view that multiple adaptive mechanisms contribute to saccadic adaptation. If adaptation were driven by a single mechanism it would need memory over several trials to estimate the consistency of the error signal. If multiple mechanisms are involved the attenuation could be assigned to the consistency-dependent interplay of the different mechanisms.

This view that multiple mechanisms are involved in saccadic adaptation was first proposed by studies of adaptation transfer (Deubel 1995; Fuchs et al. 1996). These results led to the distributed rate model of Gancarz and Grossberg (1999). In this model adaptation takes place in the cerebellum and an additional cortical locus involving the prefrontal cortex and parietal cortex. Recently, experimental studies examining the interplay between adaptation and deadaptation provided arguments for the existence of several timescales in an adaptation process (Robinson et al. 2006). In optimal control models the interplay of at least two timescales was reproduced (Smith et al. 2006). The stochastic closed loop models of Chen-Harris et al. (2008) and Ethier et al. (2008) suggest an assignment of error to two distinct mechanisms, depending on the error size. Furthermore, several electrophysiological and lesion studies suggest the cerebellum as a possible locus for adaptation (Barash et al. 1999; MacAskill et al. 2002). Subjects with lesions in the cerebellum were able to adapt, but with much slower adaptation rates. Therefore an additional pathway including the basal ganglia for adaptation on a slower timescale was suggested. In our study, the different consistency conditions could have activated the two systems to a different extent. A further aspect, stated in Barash et al. (1999) is that variance in the saccade amplitudes could be different for these two systems mentioned. However, in our study no differences in the variance of the saccade amplitude were observed.

To summarize, our study shows that the rate of saccadic adaptation depends on the consistency of the visual error in addition to its size. For both inward and outward adaptation the

rate of adaptation decreases if the error becomes inconsistent. This decrease provides evidence against a linear weighting of errors in a single adaptation mechanism. Either a nonlinear weighting of errors must occur or multiple consistency or error size dependent adaptation mechanisms must exist.

#### GRANTS

This work was supported by German Science Foundation Grant DFG LA-952/3 to M. Lappe, German Federal Ministry of Education and Research Project Visuo-spatial Cognition, and European Commission Project FP7-ICT-217077-Eyeshots.

#### DISCLOSURES

No conflicts of interest are declared by the authors.

#### REFERENCES

- Barash S, Melikyan A, Sivakov A, Zhang M, Glickstein M, Thier P. Saccadic dysmetria and adaptation after lesions of the cerebellar cortex. *J Neurosci* 19: 10931–10939, 1999.
- Bonnetblanc F, Baraduc P. Saccadic adaptation without retinal postsaccadic error. *Neuroreport* 18: 1399–1402, 2007.
- Burge J, Ernst MO, Banks MS. The statistical determinants of adaptation rate in human reaching. *J Vis* 8: Article 20 (11399–19), 2008.
- Chen-Harris H, Joiner WM, Ethier V, Zee DS, Shadmehr R. Adaptive control of saccades via internal feedback. *J Neurosci* 28: 2804–2813, 2008.
- Collins T, Rolfs M, Deubel H, Cavanagh P. Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *J Vis* 9: 1–9, 2009.
- Dean P, Mayhew JEW, Langdon P. Learning and maintaining saccadic accuracy: a model of Brainstem–Cerebellar interactions. *J Cogn Neurosci* 6: 117–138, 1994.
- Deubel H. Separate adaptive mechanisms for the control of reactive and volitional saccadic eye movements. *Vision Res* 35: 3529–3540, 1995.
- Deubel H, Wolf W, Hauske G. Adaptive gain control of saccadic eye movements. *Hum Biol* 5: 245–253, 1986.
- Ethier V, Zee DS, Shadmehr R. Changes in control of saccades during gain adaptation. *J Neurosci* 28: 13929–13937, 2008.
- Fuchs AF, Reiner D, Pong M. Transfer of gain changes from targeting to other types of saccade in the monkey: constraints on possible sites of saccadic gain adaptation. *J Neurophysiol* 76: 2522–2535, 1996.
- Gancarz G, Grossberg S. A neural model of saccadic eye movement control explains task-specific adaptation. *Vision Res* 39: 3123–3143, 1999.
- Harris CM, Wolpert DM. The main sequence of saccades optimizes speed–accuracy trade-off. *Biol Cybern* 95: 21–29, 2006.
- Henson DB. Investigation into corrective saccadic eye movements for refixation amplitudes of 10 degrees and below. *Vision Res* 19: 57–61, 1979.
- Hopp JJ, Fuchs AF. The characteristics and neuronal substrate of saccadic eye movement plasticity. *Prog Neurobiol* 72: 27–53, 2004.
- Kording KP, Wolpert DM. Bayesian integration in sensorimotor learning. *Nature* 427: 244–247, 2004.
- Lewis RF, Zee DS, Hayman MR, Tamargo RJ. Oculomotor function in the rhesus monkey after deafferentation of the extraocular muscles. *Exp Brain Res* 141: 349–358, 2001.
- MacAskill MR, Anderson TJ, Jones RD. Saccadic adaptation in neurological disorders. *Prog Brain Res* 140: 417–431, 2002.
- McLaughlin SC. Parametric adjustment in saccadic eye movements. *Percept Psychophys* 2: 359–362, 1967.
- Noto CT, Robinson FR. Visual error is the stimulus for saccade gain adaptation. *Cogn Brain Res* 12: 301–305, 2001.
- Noto CT, Watanabe S, Fuchs AF. Characteristics of simian adaptation fields produced by behavioral changes in saccade size and direction. *J Neurophysiol* 81: 2798–2813, 1999.
- Panouilleres M, Weiss T, Urquizar C, Salemme R, Munoz DP, Pelisson D. Behavioral evidence of separate adaptation mechanisms controlling saccade amplitude lengthening and shortening. *J Neurophysiol* 101: 1550–1559, 2009.
- Robinson F, Noto C, Bevans S. Effect of visual error size on saccade adaptation in monkey. *J Neurophysiol* 90: 1235–1244, 2003.



- Robinson FR, Soetedjo R, Noto C.** Distinct short-term and long-term adaptation to reduce saccade size in monkey. *J Neurophysiol* 96: 1030–1041, 2006.
- Smith MA, Ghazizadeh A, Shadmehr R.** Interacting adaptive processes with different timescales underly short-term motor learning. *PLoS Biol* 4: 1035–1043, 2006.
- Srimal R, Diedrichsen J, Ryklin EB, Curtis CE.** Obligatory adaptation of saccade gains. *J Neurophysiol* 99: 1554–1558, 2008.
- Wallman J, Fuchs AF.** Saccadic gain modification: visual error drives motor adaptation. *J Neurophysiol* 80: 2405–2416, 1998.
- Wei K, Kording K.** Relevance of error: what drives motor adaptation? *J Neurophysiol* 101: 655–664, 2009.