

Saccadic adaptation induced by a perceptual task

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The human motor system and muscles are subject to fluctuations in the short and long term. Motor adaptation is classically thought of as a low-level process that compensates for the error between predicted and executed movements in order to maintain movement accuracy. Contrary to a low-level account, accurate movements might be only a means to support high-level behavioral and perceptual goals. To isolate the influence of high-level goals in adaptation of saccadic eye movements, we manipulated perceptual task requirements in the absence of low-level errors. Observers had to discriminate one character within a peripheral array of characters. Between trials, the location of this character within the array was changed. This manipulation led to an immediate strategic change and a slower, gradual adaptation of saccade amplitude and direction. These changes had a similar magnitude to classical saccade adaptation and transferred at least partially to reactive saccades without a perceptual task. These results suggest that a perceptual task can modify oculomotor commands by generating a top-down error signal in saccade maps just like a bottom-up visual position error. Hence saccade adaptation not only maintains saccadic targeting accuracy, but also optimizes gaze behavior for the behavioral goal, showing that perception shapes even low-level oculomotor mechanisms.

(Stergiou & Decker, 2011; Sternad, Abe, Hu, & Muller, 2011). Such accurate movements are only possible because short-term adaptation of motor commands compensates for ongoing fluctuations in the accuracy of movement planning or execution (Shadmehr, Smith, & Krakauer, 2010). This is especially the case for saccadic eye movements, which are ballistic movements that do not allow for online corrections (Leigh & Zee, 1999).

Adaptation of saccadic eye movements is classically studied with the double-step paradigm, in which the saccade target is displaced during the saccade to introduce a postsaccadic error (McLaughlin, 1967). This procedure leads to adaptive changes in saccade amplitude, direction, and dynamics within several dozens of trials (Pelisson, Alahyane, Panouilleres, & Tilikete, 2010). Previous research showed that this adaptation is driven by the peri- (Panouilleres, Gaveau, Socasau, Urquizar, & Pelisson, 2013) or postsaccadic visual error of the eye-movement target but not by corrective saccades (Wallman & Fuchs, 1998; Bahcall & Kowler, 2000), proprioception (Lewis, Zee, Hayman, & Tamargo, 2001), or the visual error of distractor objects or the scene background (Madelain, Harwood, Herman, & Wallman, 2010; Madelain, Herman, & Harwood, 2013). In all these studies, a mismatch between predicted and actual saccade target position was experimentally induced by an intrasaccadic step or size change (Lavergne, Vergilino-Perez, Collins, & Dore-Mazars, 2010). Consistently, saccade adaptation is believed to be a low-level mechanism that corrects variable and systematic errors in the oculomotor system in order to maintain high accuracy of saccade targeting (Pelisson et al., 2010; Albert, Catz, Thier, & Kording, 2012). Saccadic eye movements, however, are

Introduction

Elite athletes, such as Roger Federer, are able to accomplish complex motor tasks with great accuracy, such as hitting a tennis ball to make it land along the court sideline, despite considerable neuromotor noise

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typically directed to behaviorally or perceptually relevant targets to project them on the fovea, the retinal area that allows high-acuity color vision. In that sense, high saccade accuracy might not be an objective in itself but only a means to achieve high perceptual performance. Thus, the ultimate purpose of saccade adaptation might be the optimization of eye-movement programming for perception.

How well eye movements are tuned to perceptual and behavioral tasks is currently debated (Schütz, Braun, & Gegenfurtner, 2011). Saccade landing points are optimal in some tasks (Najemnik & Geisler, 2005) but not in others (Morvan & Maloney, 2012), and in some tasks, optimal and suboptimal eye-movement behavior depends on saccade latency (Schütz, Trommershäuser, & Gegenfurtner, 2012). Studies involving learning usually investigated long-term effects like the acquisition of a new sensory-motor skill (Sailer, Flanagan, & Johansson, 2005) or the acquisition of a new preferred retinal locus after foveal lesions (Heinen & Skavenski, 1992; Michel & Geisler, 2009). Hence, it has never been investigated whether short-term saccade adaptation only maintains saccade accuracy or whether it serves visual perception in a more global sense. In the latter case, the specific requirements of a perceptual task alone should be able to drive adaptation. We therefore asked whether saccadic eye movements could be adapted by the requirements of a perceptual task without any peri-saccadic displacement of the saccade target.

Method

Design

To measure the influence of a perceptual task on saccade amplitudes, we asked observers to discriminate one character that was presented within a peripheral array of characters. We designed the discrimination task to require foveal acuity, such that observers had to saccade to the character array to solve the task. To induce saccadic adaptation, the discrimination character was presented at different locations within the peripheral array in different blocks of trials. This manipulation does not induce a bottom-up visual error because the character array itself did not change its location, and the location of the discrimination character is only relevant in relation to the demands of the perceptual task.

Observers

Forty-eight students from Giessen University (36 female, ages between 19 and 38) participated in these

experiments. Experiments were in accordance with the principles of the Declaration of Helsinki and approved by the local ethics committee LEK FB06 at Giessen University (Proposal Number 2009-0008). We had to exclude the data of five observers because more than 30% of trials had to be excluded (cf. eye-movement recording). To allow within-subjects comparisons, the same nine observers participated in experiments 1–3. Also, the same 11 observers participated in experiments 4 and 5.

Visual stimuli

Discrimination targets were digital characters 2, 5, 3, E, and 8. The characters were displayed in black or white in front of a random noise background extending 0.175° beyond the characters. The character contrast was 0.2, and the noise contrast was 0.5 except for experiments 4 and 5, in which the character contrast was 0.25. The characters had a size of $0.35^\circ \times 0.70^\circ$ and a gap of 0.35° . In on-axis adaptation experiments 1–3 and 6, seven characters were aligned horizontally for a total width of 4.9° ; in cross-axis adaptation experiments 4 and 5, five characters were aligned vertically for a total height of 5.25° . The fixation target was a character 8 except in experiments 6 and 7, in which a character 8, a filled white, and a filled yellow rectangle were used as fixation targets.

Experimental procedure

Observers had to fixate a fixation target. After 500 to 1000 ms, the fixation target disappeared and a peripheral character array appeared at an eccentricity of 9° , randomly to the right or to the left except when the fixation target reached the farthest position to the left or to the right. Until saccade onset, all characters were 8s and displayed in white. After saccade onset, all characters turned randomly into 2, 3, 5, or E. One of them was the discrimination character and was displayed in black. In experiments with a perceptual task, observers had to press a corresponding button on a keyboard. The character array disappeared 100 ms after saccade onset, and 1500 ms after saccade onset, observers heard a beep if their judgment was incorrect. A new fixation target appeared at the previous center of the character array, such that the character array performed a random walk across five potential positions on the monitor during the experiment (Figure 1). Breaks of 30 s occurred every 100 trials, and observers were advised to close their eyes during the breaks. Observers were also instructed that the location of the discrimination character remained identical within each block of 100 trials in experiments with a

perceptual task. In experiments without a perceptual task, observers were merely instructed to saccade to the peripheral array without mentioning the single characters in the peripheral array.

Materials

Stimuli were displayed on a 21-in. SONY GDM-F520 CRT monitor driven by a Nvidia Quadro NVS 290 graphics board with a refresh rate of 100 Hz noninterlaced. At a viewing distance of 47 cm, the active screen area subtended 45° horizontally and 36° vertically. With a spatial resolution of 1280 × 1024 pixels, this results in 28 pixels/°. The luminance of white, gray, and black pixels was 87, 14.6, and 0.04 cd/m², respectively. Stimulus presentation was controlled by Matlab, using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997).

Eye-movement recording

Eye position signals of the right eye were recorded with a video-based eye tracker (EyeLink 1000; SR Research, Ottawa, Ontario, Canada) and were sampled at 1000 Hz. The eye tracker was driven by the EyeLink toolbox (Cornelissen, Peters, & Palmer, 2002). Saccade onsets were detected online when eye velocity of two subsequent samples exceeded 50 and 100°/s, respectively. For offline analysis, the EyeLink saccade parser was used with a velocity and acceleration threshold of 22°/s and 3800°/s², respectively. Saccade curvature was estimated using a quadratic fit (Ludwig & Gilchrist, 2002). We excluded, on average, 14.35% of trials if no saccade onset was detected after 2 s (3.05%) and if the saccade amplitude was smaller than 5° or larger than 13° (13.97%).

Experiments

We measured saccadic eye movements in eight different experiments. If observers participated in several experiments, the sessions were at least separated by one week.

Perceptual task

In experiment 1 ($n = 9$), the character array was oriented horizontally (on-axis adaptation), and observers had to perform a perceptual task. In the first 100 and last 300 trials, the discrimination character was located at the central location (position four) in the array (Figure 1A). In the 300 trials in between, the discrimination character was located at eccentric

locations (position two or six, counterbalanced between observers), such that saccades had to be shortened in one direction and prolonged in the other direction (Figure 1B, C).

No task

In experiment 2 ($n = 9$), the observers saw the same stimuli as in experiment 1 but did not have to perform the perceptual task.

Classical adaptation

In experiment 3 ($n = 9$), the whole character array was shifted peri-saccadically in the adaptation phase to induce a classical saccade adaptation. The size of the peri-saccadic shift was 1.4° and identical to the distance between the central (position four) and eccentric character locations (positions two or six). The black discrimination character appeared always at the central location in the array.

Cross-axis adaptation, perceptual task

In experiment 4 ($n = 11$), we tested cross-axis adaptation. To this end, the character array was oriented vertically, and the observers had to perform the perceptual task.

Cross-axis adaptation, no task

In experiment 5 ($n = 11$), the observers saw the same stimuli as in experiment 4 but did not have to perform the perceptual task. In both cross-axis experiments, we analyzed the amplitude of the vertical component of the saccade, which we call vertical amplitude.

Transfer of adaptation

In experiment 6 ($n = 10$), we tested the transfer of adaptation to different types of saccades. In the first 150 trials, perceptual task, reactive and voluntary conditions were interleaved. In the reactive condition, the fixation target was a filled grey rectangle that disappeared when the character array appeared. In the voluntary condition, the character array appeared at the beginning of the trial, and observers were instructed to look at it when the fixation target turned from a filled rectangle to a character 8. In the reactive and voluntary conditions, the peripheral character array contained only digital character 8. In the perceptual task condition, the fixation target was a yellow filled rectangle that also disappeared when the character array appeared. In the first 150 trials, the discrimination character was at the central location in the array. Afterward, there were 300 trials with the perceptual

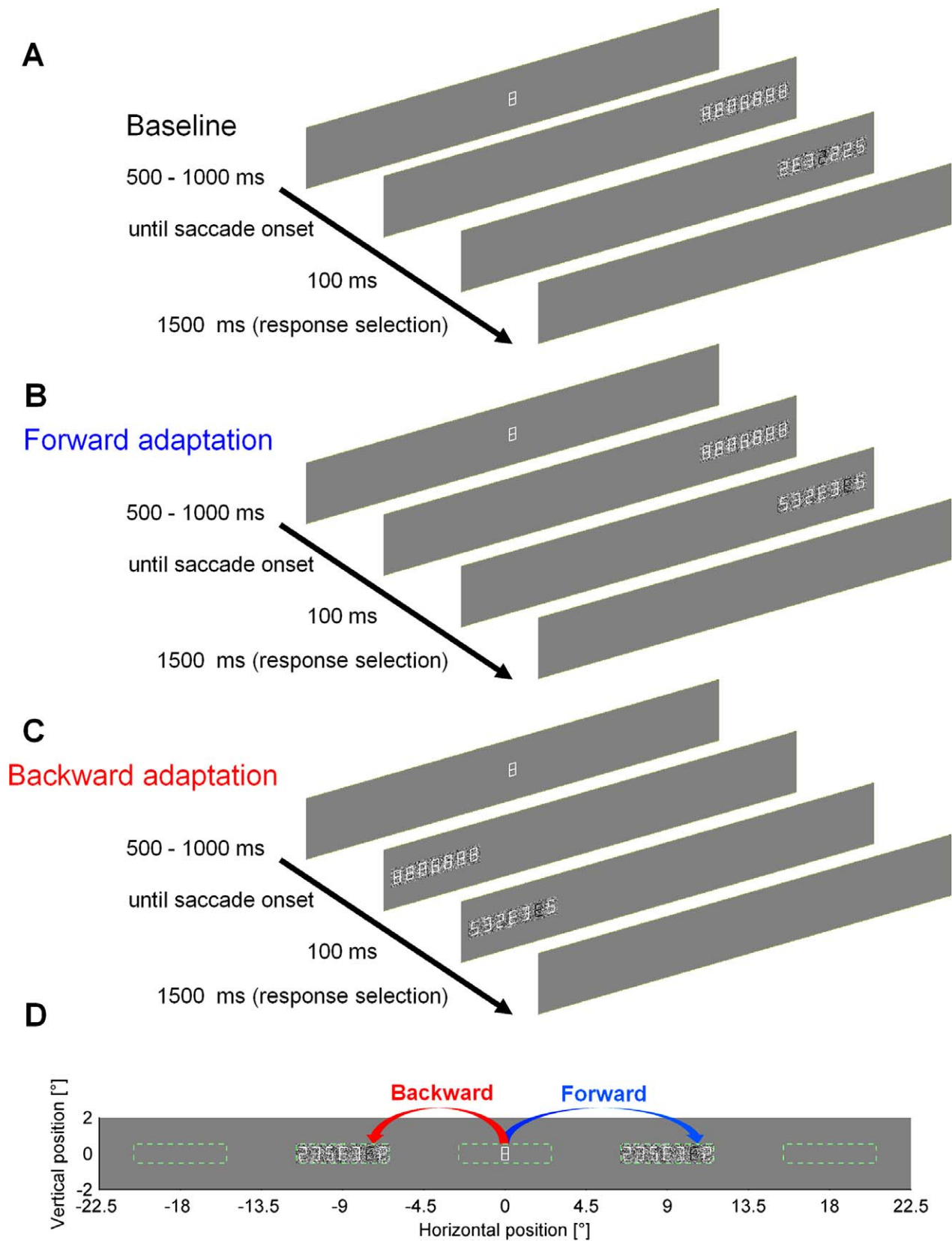


Figure 1. Experimental paradigm. (A) Time course of one baseline trial. Observers had to look at a peripheral character array and to discriminate the black discrimination character, which was displayed for 100 ms after saccade detection. In 100 pre- and 300 postadaptation trials, the discrimination character was always located at the center of the peripheral array. (B) Time course of one

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forward adaptation trial. In 300 adaptation trials, the discrimination character was located at an eccentric location in the array. The eccentric location is further away from initial fixation, such that saccade amplitudes have to be increased. (C) Time course of one backward adaptation trial. The eccentric location is closer to initial fixation, such that saccade amplitudes have to be decreased. (D) Spatial layout. The peripheral array could appear on one of the five positions, indicated by the green dashed lines, but always adjacent to the position of initial fixation. Depending on the direction of the saccade, an eccentric location of the discrimination character leads to forward or backward adaptation as indicated by the colored arrows.

task, in which the discrimination character was at eccentric locations in the character array. Finally, there were 150 trials with the perceptual task, reactive and voluntary conditions interleaved. To maintain adaptation, the discrimination character remained at eccentric locations in the trials with the perceptual task.

Experiment 7 ($n = 10$) was a control experiment, in which trials with and without the perceptual task were presented in different blocks. In the first 100 trials, reactive and voluntary conditions without the perceptual task were interleaved randomly. This was followed by 50 trials with the perceptual task at the center of the character array and 300 trials with the perceptual task at eccentric locations in the character array. After this adaptation phase, there were again 100 trials of reactive and voluntary conditions without the perceptual task followed by 50 trials with the perceptual task at eccentric locations. Observers were instructed that trials with and without the perceptual task are presented in separate blocks of trials.

Presaccade cue control

Experiment 8 ($n = 9$) was identical to experiment 1 with the exception that the presaccadic mask at the location of the discrimination character was also drawn in black, such that there was no ambiguity about the location of the discrimination character.

Data analysis and modeling

We used the average saccade parameter values in the 50 preadaptation trials and in the last 50 adaptation trials to quantify the effects of adaptation on eye movements. The effects of experimental condition, adaptation phase, and saccade direction were statistically tested by repeated-measures ANOVA. Descriptive statistics include the mean and standard deviation across observers.

To estimate the relative contributions of an immediate strategic adjustment of saccades and a slow, gradual saccade adaptation, we extended a state-space model that has been used successfully to model saccade adaptation (Srimal, Diedrichsen, Ryklin, & Curtis, 2008). We assume that the gain of a saccade y_n in a given trial n is determined by a weighted combination

of the state of an immediately adapting process z_i and the state of a slowly adapting process z_s .

$$y_n = I z_{i,n} + (1 - I) z_{s,n} \quad (1)$$

The relative weight of the immediate and slow process is determined by I .

The state of the slow process is updated every trial by a certain proportion S of the difference between the adaptation state and the target position u_n .

$$z_{s,(n+1)} = z_{s,n} - S(z_{s,n} - u_n) \quad (2)$$

The state of the immediate process is also updated every trial but by the full difference between the adaptation state and the target position.

$$z_{i,(n+1)} = z_{i,n} - (z_{i,n} - u_n) \quad (3)$$

Because there was a strong undershoot in the preadaptation trials, we removed the average difference between target position and saccade amplitude in the preadaptation trials from the target position for the model estimation. The initial gain was estimated as the average saccade amplitude in the first 10 trials.

The primary purpose of the model was to distinguish between an immediate adjustment and a slow adaptation. Hence, the model is limited and does not contain differential learning rates for forward and backward adaptation (Ethier, Zee, & Shadmehr, 2008a) and also does not capture spontaneous recovery (Ethier, Zee, & Shadmehr, 2008b).

To test the contribution of the immediate adjustment and the slow adaptation, we fitted two reduced one-parameter models that used only one of these two parameters: either the immediate adjustment or the gradual adaptation. We also used a null model, which has neither immediate adjustment nor gradual adaptation. For each of the four models, we calculated the Bayesian information criterion (BIC), which takes into account the residual sum of squares (RSS), the number of free parameters k , and the number of observations n (Schwarz, 1978).

$$BIC = n \ln(RSS/n) + k \ln(n) \quad (4)$$

We calculated the difference between the individual BIC values and the lowest value (Burnham & Anderson, 2002) because the absolute value of the BIC is not meaningful.

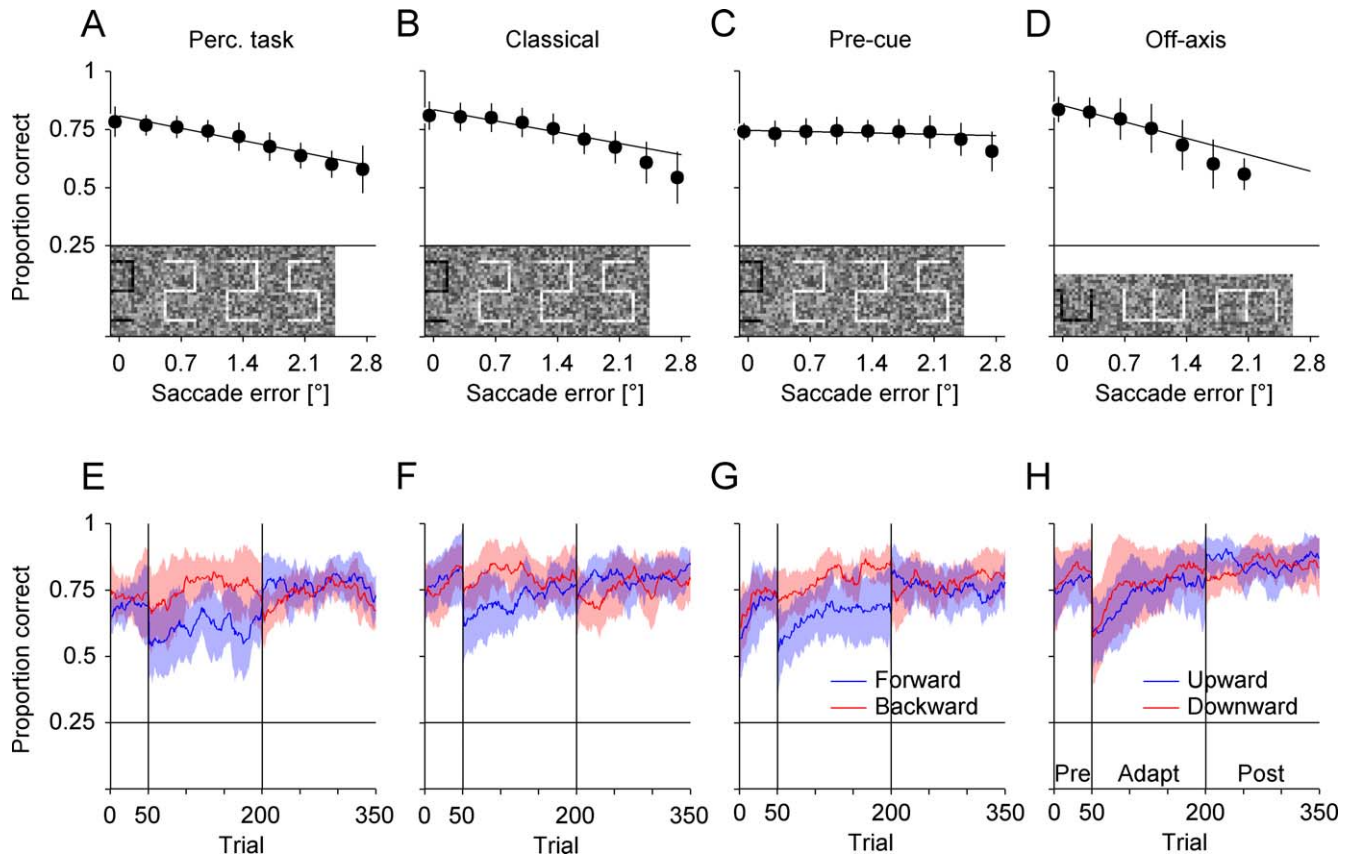


Figure 2. Perceptual results. (A–D) Perceptual performance as a function of absolute saccade error relative to the location of the discrimination character. The black line represents a linear regression. (E–H) Perceptual performance as a function of trial number. Data are smoothed by a running average with a bin size of 25 trials. (E–G) Forward and backward adaptations are shown in blue and red, respectively. (H) Upward and downward adaptation are shown in blue and red, respectively. (A–H) Error bars represent 95% confidence intervals. The black horizontal line indicates chance performance of 25%.

$$\Delta BIC_i = BIC_i - BIC_{\min} \quad (5)$$

Finally, we calculated the relative weights for each model (Burnham & Anderson, 2002). This relative likelihood estimates which model is most likely the “true” model, given the data.

$$p_i = e^{-0.5\Delta BIC_i} / \sum_{r=1}^R e^{-0.5\Delta BIC_r} \quad (6)$$

Results

In the first experiment, observers were instructed to look at a peripherally displayed array of seven characters and to discriminate one of them. The discrimination character was displayed in black, all others in white (Figure 1A). The perceptual task required foveal acuity because performance decreased from 78% correct at a retinal error of 0° to 58% correct at an error of 2.8° (Figure 2A). A linear regression

showed a negative relationship between retinal error and perceptual performance (slope -0.08 ± 0.03 , $t(8) = 8.23$, $p < 0.001$). To study learning in the eye-movement system, we changed the location of the discrimination character. In pre- and postadaptation trials, the discrimination character was always located at the center of the array. In adaptation trials, the discrimination character was always located at a peripheral location in the array. For instance, the eccentricity was larger (forward) for rightward saccades and smaller (backward) for leftward saccades (Figure 1B, C). There was no bottom-up visual error because the character array itself did not change its location. The location of the discrimination character within the character array became only relevant because of the instructions to perform a perceptual task.

In general, the measured saccade amplitudes showed the typical undershoot of more than 10% (Harris, 1995), but there was also a clear effect of the location of the discrimination character (Figures 3A, S1, and S2): In the preadaptation phase, saccade amplitudes were similar for both directions (forward: $7.73^\circ \pm 0.40^\circ$; backward $7.91^\circ \pm 0.48^\circ$). At the end of the adaptation

phase, saccade amplitudes were increased in the forward direction ($8.65^\circ \pm 0.59^\circ$) and decreased in the backward direction ($7.17^\circ \pm 0.33^\circ$). This was supported by a significant interaction between phase and direction, $F(1, 8) = 70.30$, $p < 0.001$. Thus, the location of the discrimination character affected saccade amplitudes although the whole character array did not change its position. The changes in saccade amplitudes were accompanied by consistent changes in saccade peak velocity (Text S1, Figure S3).

If saccade targeting would maximize the intake of information, one could expect an immediate adjustment of saccade amplitudes to the new location of the discrimination character. Indeed, the average traces in Figure 3A show a sudden change of saccade amplitudes at the onset and offset of the adaptation phase. To quantify the relative contributions of a strategic, immediate adjustment and a slower, gradual adaptation of saccade amplitudes, we fitted a state-space model with two parameters. State-space models are commonly used to model motor learning (Thoroughman & Shadmehr, 2000; Srimal et al., 2008). In this model, the strategic weight I (Figure 3E) quantifies how much of the distance to the discrimination character is compensated immediately. The adaptation rate S (Figure 3F) quantifies how much of the distance to the discrimination character is adapted over time. We also fitted two one-parameter models, in which either the immediate adjustment or the slow adaptation was fixed to zero, and a zero-parameter model, in which amplitudes did not change. To determine which of these models is most likely given the data, we first calculated the BIC for each model (Schwarz, 1978), then calculated the likelihood of each model, and normalized these likelihoods such that they added up to 100% (Burnham & Anderson, 2002). The two-parameter model had a higher relative likelihood than the one- or zero-parameter models ($91.40\% \pm 13.33\%$) (Table S1). This means that both parameters were necessary to account for the data. The two-parameter model revealed that $26.65\% \pm 13.30\%$ of the distance to the discrimination character was compensated by an immediate adjustment, and this was significantly larger than zero, $t(8) = 6.01$, $p < 0.001$. In every trial, $0.63\% \pm 0.58\%$ of the distance was compensated by slow adaptation, $t(8) = 3.27$, $p = 0.011$. Over the course of 150 adaptation trials, the slow adaptation compensates $36.58\% \pm 18.96\%$ of the distance to the discrimination character, which is comparable to the compensation by the strategic adjustment, $t(8) = 1.24$, $p = 0.252$. In conclusion, the higher likelihood of the two-parameter model and the fitted parameters indicate an immediate strategic adjustment and a slow, gradual adaptation of saccade amplitudes.

If saccade amplitudes were actually modified to support the perceptual task, the changes in saccade

amplitudes should also be reflected in perceptual performance. We analyzed performance in the 50 preadaptation trials and the first and last 50 adaptation trials (Figure 2E). In the forward direction, perceptual performance decreased at the beginning of the adaptation phase from $69\% \pm 1\%$ to $58\% \pm 3\%$. At the end of the adaptation phase, it increased to $62\% \pm 2\%$, $F(2, 16) = 4.15$, $p = 0.035$. These effects are consistent with the changes in saccade error due to the manipulation of the discrimination location and the following adaptation of saccade amplitude. In the backward direction, perceptual performance remained stable throughout the adaptation phase: pre: $73\% \pm 2\%$; beginning: $72\% \pm 2\%$; end: $76\% \pm 3\%$; $F(2, 16) = 0.28$, $p = 0.756$. This does not contradict the adaptation of amplitudes because there was a saccade undershoot at the beginning of the experiment, and the eccentric discrimination location actually brought the discrimination character closer to the saccade landing position.

One strategy to increase voluntary control of saccade targeting is to delay the saccades as shown previously for the integration of salience and value information (Schütz et al., 2012). Saccade latency in the on-axis experiment with the perceptual task was 133.97 ± 12.19 ms. The main effects of phase and direction and the two-way interaction were not significant (all F s < 1.335 ; all p s > 0.281). Hence, the observers did not change their saccade latency during this experiment.

Experiment without the perceptual task (experiment 2)

In the previous experiment, the pre- and postadaptation phases differed by the location of the black discrimination character within the character array. To distinguish the influence of the perceptual task from purely visual effects, we displayed the same stimuli, but observers did not have to perform the perceptual task (Figures 3B and S2). As with the perceptual task, saccade amplitudes were similar in both directions in the preadaptation phase (forward: $7.83^\circ \pm 0.42^\circ$; backward: $8.01^\circ \pm 0.55^\circ$). However, there was also no difference at the end of the adaptation phase (forward: $7.87^\circ \pm 0.53^\circ$; backward $7.56^\circ \pm 0.64^\circ$). Consistently, there was only a trend for an interaction between phase and direction, $F(1, 8) = 4.39$, $p = 0.070$. Moreover, the three-way interaction between task (perceptual vs. no task), phase, and direction was highly significant, $F(1, 8) = 17.06$, $p = 0.003$, indicating that the effect of phase depended on the presence of a concurrent perceptual task.

None of the state-space models was clearly superior to explain the data. The highest relative likelihood was achieved by the two-parameter model ($42.74\% \pm 49.57\%$), followed by the zero-parameter model without amplitude change ($35.39\% \pm 43.96\%$) and the one-

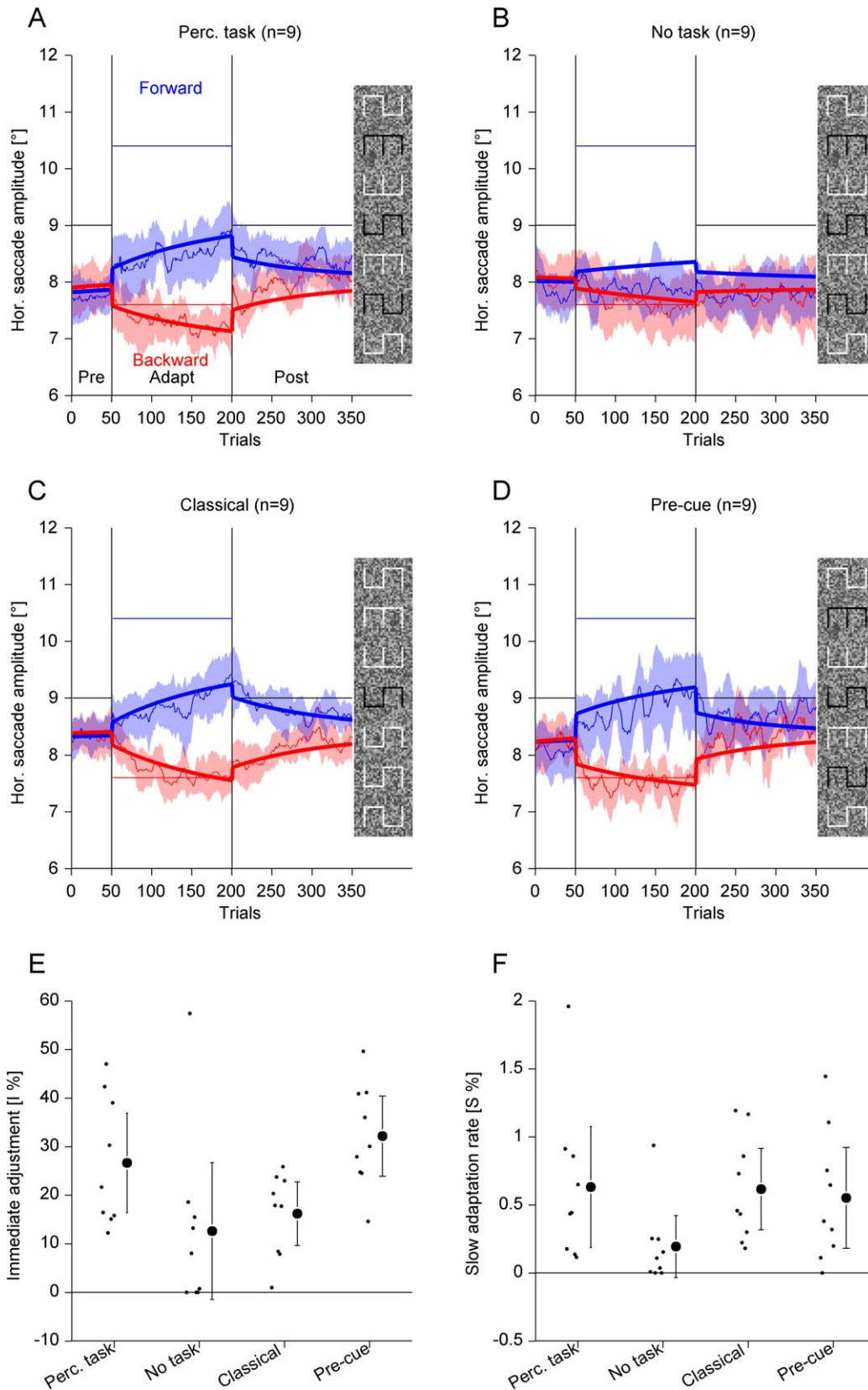


Figure 3. On-axis adaptation. (A) Experiment 1 with a perceptual task. (B) Experiment 2 without a perceptual task. (C) Experiment 3, classical adaptation with intrasaccadic position change and a perceptual task. The discrimination character was always located at the central location of the character array, and the whole array was moved during the saccade. (D) Experiment 8 with a perceptual task

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and a precue. The presaccadic mask at the location of the discrimination character was drawn in black. (A–D) The thin lines represent the average across observers. Data are smoothed by a running average with a bin size of 10 trials. The shaded regions represent 95% confidence intervals. The thick lines represent the two-parameter model fit. Forward and backward adaptations are shown in blue and red, respectively. The vertical lines indicate the onset and offset of the adaptation phase. The horizontal lines indicate the location of the discrimination character. (E) Immediate adjustment in the two-parameter model fits. (F) Slow adaptation rate in the two-parameter model fits. (E & F) Small dots represent data for individual observers; large dots represent the mean across observers; error bars represent 95% confidence intervals.

parameter models with slow adaptation ($15.36\% \pm 31.03\%$) or immediate adjustment ($6.51\% \pm 15.76\%$). This means there were no consistent effects of immediate adjustment and slow adaptation without the perceptual task. This is also reflected in the parameter values of the two-parameter model (Figure 3E, F). The immediate adjustment was $12.60\% \pm 18.34\%$, not significantly different from zero, $t(8) = 2.06$, $p = 0.073$, but significantly smaller than with the perceptual task, $t(8) = 2.32$, $p = 0.049$. The slow adaptation rate was $0.19\% \pm 0.30\%$, not significantly different from zero, $t(8) = 1.96$, $p = 0.085$, but significantly smaller than with the perceptual task, $t(8) = 3.57$, $p = 0.007$. Hence, both the immediate adjustment and the slow adaptation were either absent or significantly smaller without than with a perceptual task.

The average saccade latency in the experiment without the perceptual task was 148.56 ± 17.58 ms and significantly longer than with the perceptual task, $t(8) = 3.04$, $p = 0.016$. This is consistent with previous reports showing that a perceptual task at the saccade target reduces saccade latencies compared to a neutral condition without task (Montagnini & Chelazzi, 2005; Trotter & Pratt, 2005; Bieg, Bresciani, Bulthoff, & Chuang, 2012). Like in the experiment with the perceptual task, the main effects of phase and direction and the two-way interaction were not significant (all F s < 2.745 ; all p s > 0.136).

Classical adaptation with an intrasaccadic position change (experiment 3)

In the classical saccade-adaptation paradigm (McLaughlin, 1967), the visual target is displaced during the saccades. In the following experiment, we tested whether our task-driven adaptation was of a similar magnitude as the classical adaptation (Figures 3C and S2). The discrimination target was always shown at the central location of the array. In the adaptation phase, the whole array was displaced forward or backward during the saccade, such that the central location had the same position as the eccentric discrimination locations in the previous experiments.

Also with the classical adaptation paradigm, the perceptual task required foveal acuity. Perceptual performance decreased from 81% correct at a retinal error of 0° to 54% correct at an error of 2.8° (Figure 2B). A linear regression showed a negative relationship between retinal error and perceptual performance (slope -0.07 ± 0.02 , $t(8) = 9.52$, $p < 0.001$).

In the preadaptation phase, saccade amplitudes were similar in both directions (forward: $8.37^\circ \pm 0.33^\circ$; backward $8.33^\circ \pm 0.37^\circ$). At the end of the post-adaptation phase, amplitudes were increased in the forward direction ($9.17^\circ \pm 0.49^\circ$) and decreased in the backward direction ($7.63^\circ \pm 0.35^\circ$). This effect of adaptation was supported by a significant interaction between phase and direction, $F(1, 8) = 48.59$, $p < 0.001$. The magnitude of adaptation was similar to the adaptation with the perceptual task, which was confirmed by the absence of a significant three-way interaction between experiment (perceptual task vs. classical adaptation), phase, and direction, $F(1, 8) = 1.50$, $p = 0.256$.

As with the perceptual task, the relative likelihood of the two-parameter model was very high ($70.62\% \pm 43.49\%$). The immediate adjustment was $16.20\% \pm 8.51\%$ (Figure 3E) and significantly smaller than with the perceptual task, $t(8) = 2.42$, $p = 0.042$. The slow adaptation rate was $0.62\% \pm 0.39\%$ (Figure 3F) and not significantly different from the experiment with the perceptual task, $t(8) = 0.10$, $p = 0.926$. These results suggest that even the classical adaptation paradigm contained an immediate adjustment and a slow adaptation process. However the immediate adjustment was smaller than with a perceptual task. Across observers, the immediate adjustment in the perceptual task and in the classical adaptation experiment were not correlated, $r(8) = 0.36$, $p = 0.172$. The slow adaptation rate reached a higher correlation, but this was only marginally significant, $r(8) = 0.52$, $p = 0.075$.

Overall changes of saccade amplitude in the perceptual task experiment and the classical adaptation experiment were highly similar. We take this as an indication that the perceptual task triggered saccade adaptation similar to the classical McLaughlin paradigm (McLaughlin, 1967).

Consistent with the changes in saccade amplitude, the perceptual performance decreased in the forward

direction at the beginning of the adaptation phase from $79\% \pm 2\%$ to $68\% \pm 3\%$ (Figure 2F). At the end of the adaptation phase, it increased to $76\% \pm 1\%$, $F(2, 16) = 7.73$, $p = 0.004$. Perceptual performance in the backward direction remained constant throughout the adaptation phase: pre: $78\% \pm 2\%$; beginning: $81\% \pm 2\%$; end: $80\% \pm 1\%$; $F(2, 16) = 0.32$, $p = 0.731$. Due to the undershoot in the preadaptation phase, a backward step brought the discrimination character closer to the saccade landing position. Hence, one would not expect a drop in performance in the backward direction.

Cross-axis adaptation (experiments 4 and 5)

Besides saccade amplitude, saccade direction is also under adaptive control (Deubel, 1987; Chen-Harris, Joiner, Ethier, Zee, & Shadmehr, 2008; Schütz & Souto, 2011). It remains unclear whether this cross-axis adaptation is based on the same mechanisms as backward or forward adaptation of saccade amplitude. Cross-axis adaptation is of particular interest for our research question because potential top-down effects are orthogonal to the normal saccade direction so that these can be studied in isolation.

To elicit cross-axis adaptation, we arranged five characters vertically. In preadaptation and postadaptation trials, the discrimination character was always located at the center. In adaptation trials, the discrimination character was located at one location above or one location below the center, depending on the direction of the saccade. For instance, when the perceptual target was located below the center for leftward saccades and above for rightward saccades, we expected to induce downward adaptation of leftward saccades and upward adaptation of rightward saccades.

Like for the horizontal arrangement, the perceptual task required foveal acuity. Perceptual performance decreased from 83% correct for a retinal error of 0° to 56% correct for an error of 2.1° (Figure 2D). A linear regression showed a negative relationship between retinal error and perceptual performance (slope -0.10 ± 0.08 , $t(10) = 4.41$, $p = 0.001$).

We analyzed the amplitude of the vertical component of the saccade to measure the influence of the perceptual task on the saccade direction (Figure 4A and S4). In the preadaptation phase, vertical saccade amplitudes were close to zero (upward: $0.04^\circ \pm 0.23^\circ$; downward: $0.02^\circ \pm 0.07^\circ$). At the end of the adaptation phase, vertical saccade amplitudes differed according to the location of the discrimination character (upward: $0.49^\circ \pm 0.41^\circ$; downward: $-0.54^\circ \pm 0.22^\circ$). This effect of adaptation was confirmed by a significant interaction between phase and direction, $F(1, 10) = 48.44$, $p < 0.001$. As in the on-axis experiments, the two-parameter model had a high relative likelihood ($83.68\% \pm 25.08\%$). The immediate

adjustment (Figure 4B) was $16.52\% \pm 10.64\%$, $t(10) = 5.15$, $p < 0.001$. The slow adaptation rate (Figure 4C) was $0.50\% \pm 0.46\%$, $t(10) = 3.56$, $p = 0.005$. The higher likelihood of the two-parameter model and the fitted parameter values indicate that also the task-driven adaptation of saccade direction contained an immediate adjustment and a slow adaptation.

Saccade trajectories can become curved during cross-axis adaptation (Chen-Harris et al., 2008; Schütz & Souto, 2011) because the initial and late saccade trajectories are controlled by independent mechanisms with different learning rates. Also, in our data, the average saccade trajectories were curved at the end of the adaptation phase (Figure 4D). We quantified this curvature by fitting a quadratic function (Ludwig & Gilchrist, 2002). We report the quadratic coefficient to indicate the direction of curvature with respect to the initial trajectory. In the preadaptation phase, saccade curvature was close to zero (upward: -0.02 ± 0.18 ; downward: -0.04 ± 0.13) (Figure 4E). At the end of the adaptation phase, saccades were curved downward in the upward condition (0.03 ± 0.15) and curved upward in the downward condition (-0.13 ± 0.15). This means that the effect of adaptation had a stronger influence on the late than on the early saccade trajectories. This effect of adaptation was supported by a significant interaction between phase and direction, $F(1, 10) = 17.42$, $p = 0.002$. These results show that the task-driven adaptation had a similar effect on saccade trajectories as the previously reported effects in classical adaptation paradigms (Chen-Harris et al., 2008; Schütz & Souto, 2011). As for the on-axis adaptation, effects on vertical saccade amplitudes and saccade trajectories were absent or significantly smaller without than with the perceptual task (Text S2 and Figures S4 and S5).

The changes in saccade direction were accompanied by consistent changes in perceptual performance over the different phases (Figure 2H), $F(2, 20) = 15.15$, $p < 0.001$. Perceptual performance dropped from preadaptation levels (upward: $79\% \pm 3\%$; downward: $82\% \pm 3\%$) at the beginning of the adaptation (upward: $64\% \pm 4\%$; downward: $71\% \pm 7\%$) and increased at the end of adaptation (upward: $82\% \pm 5\%$; downward: $85\% \pm 2\%$). Hence the adaptation of saccade direction improved performance in the perceptual task in the upward and the downward directions.

Transfer of adaptation to reactive and voluntary saccades without the perceptual task (experiments 6 and 7)

Saccadic eye movements can be triggered reactively by the sudden appearance of a peripheral stimulus or voluntarily by a conscious decision. These different

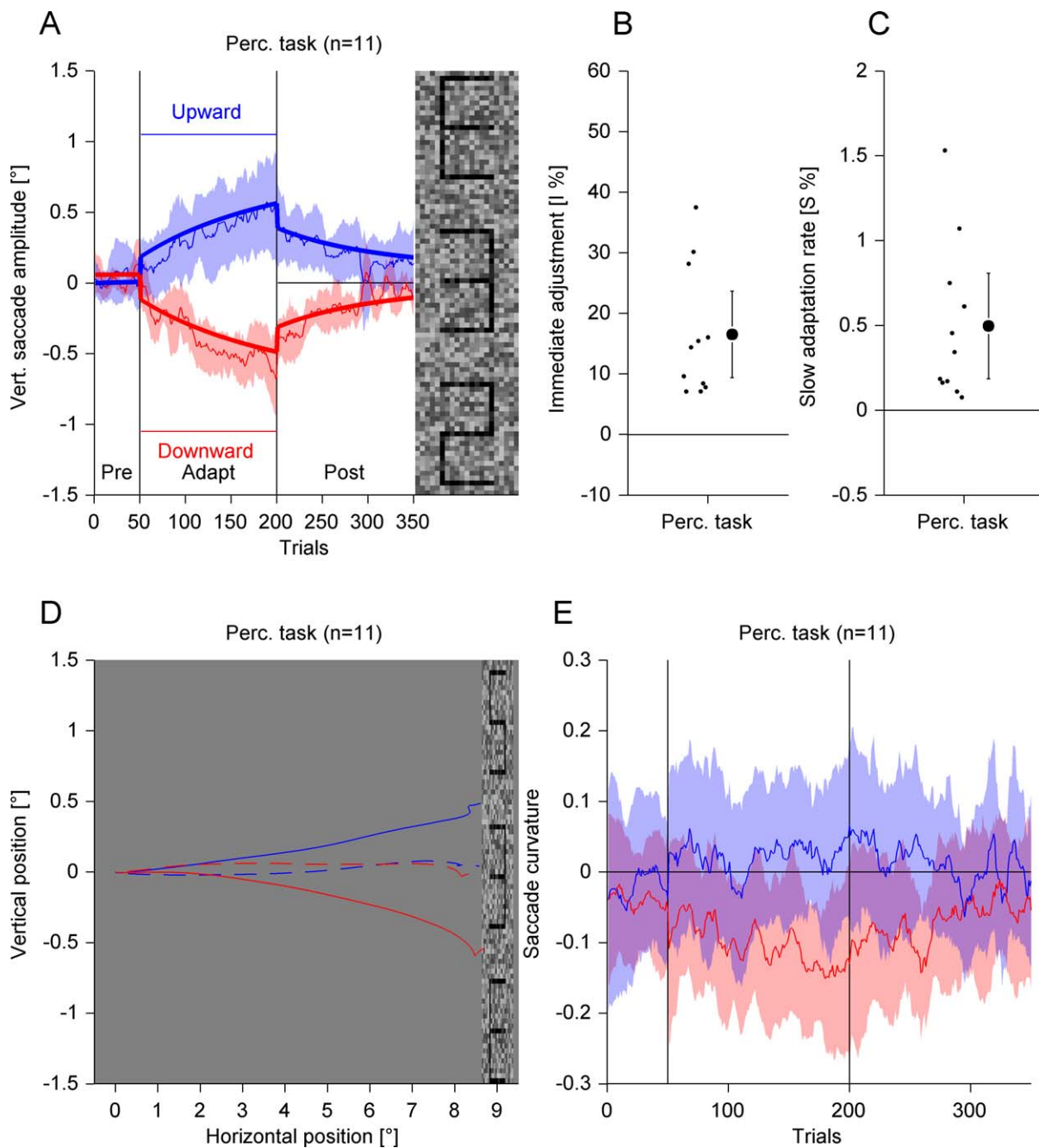


Figure 4. Experiment 4, cross-axis adaptation with a perceptual task. (A) Vertical saccade amplitude. Conventions are the same as in Figure 3A. (B) Immediate adjustment in the two-parameter model fits. Conventions are the same as in Figure 3E. (C) Slow adaptation rate in the two-parameter model fits. Conventions are the same as in Figure 3F. (D) Average saccade trajectories in the preadaptation phase (dashed lines) and at the end of the adaptation phase (solid lines). Note that the x-axis scale is compressed. (E) Saccade curvature. Positive values indicate trajectory deviations (curvature) downward.

types of saccades are partially supported by different neural structures (Mort et al., 2003) and show only partial transfer of saccade adaptation (Hopp & Fuchs, 2010; Pelisson et al., 2010). The transfer of saccade adaptation is a useful tool to test whether different types of saccades are adapted by the same or different neural circuitry. Furthermore, if the perceptual task

actually induces saccade adaptation, it should show some transfer to regular saccades without a perceptual task. The nature of the saccades in our perceptual task is unclear and transfer could happen to reactive and/or voluntary saccades. The peripheral character array and the fixation target appeared and disappeared at the same time, favoring reactive saccades, as confirmed by

short latencies below 150 ms on average. However, observers had to perform a perceptual task at the saccade target and had the possibility to strategically adjust their saccade amplitudes according to the location of the discrimination character.

In experiment 6, we investigated whether the adaptation with the perceptual task transfers to reactive and voluntary saccades, both without a perceptual task. To elicit reactive saccades, the peripheral character array appeared at the same time as the fixation target disappeared. To elicit voluntary saccades, the peripheral character array appeared already at the beginning of the trial, but observers were only allowed to look at it when the fixation target changed its shape. In both cases, no perceptual discrimination was required. In the first 150 trials, we interleaved perceptual task and reactive and voluntary conditions to estimate baseline saccade amplitudes. This was followed by 300 perceptual task trials, in which the discrimination character had the same eccentric horizontal location as in the first experiment. At the end, there were 150 trials with the perceptual task and reactive and voluntary conditions interleaved.

We successfully induced a similar adaptation effect with the perceptual task as in the previous experiments (Figures 5A and S6). The two-parameter model reached a high relative likelihood ($83.32\% \pm 21.28\%$). The immediate adjustment was $28.91\% \pm 16.16\%$ (Figure 5B) and significantly larger than zero, $t(9) = 5.66$, $p = 0.001$. The slow adaptation rate was $0.39\% \pm 0.19\%$ (Figure 5C) and also significantly larger than zero, $t(9) = 6.48$, $p < 0.001$.

To confirm that our manipulation of saccade type was successful, we checked that voluntary saccades had longer latencies than reactive saccades (Walker, Walker, Husain, & Kennard, 2000). Saccade latencies (Figure 5D) with the perceptual task (149.05 ± 19.63 ms) and in the reactive condition (156.98 ± 24.93 ms) were similar, $t(9) = 1.70$, $p = 0.123$, and highly correlated, $r(9) = 0.81$, $p = 0.002$. As expected, the voluntary condition produced the longest saccade latencies (416.88 ± 161.72 ms), which were significantly longer than with the perceptual task, $t(9) = 5.29$, $p = 0.001$, and the reactive condition, $t(9) = 5.04$, $p = 0.001$. Latencies were also not correlated between the voluntary condition and the other conditions (all r s < 0.14 , all p s > 0.347). Hence saccade latencies were very similar in the task and the reactive condition but clearly distinct from the voluntary condition.

To estimate the adaptation magnitude and its transfer to reactive and voluntary saccades, we calculated the difference between saccade amplitudes in the preadaptation trials and at the end of the experiment, separately for forward and backward directions. With the perceptual task, saccade amplitudes increased significantly in the forward direction,

$13.62\% \pm 5.42\%$; $t(9) = 7.94$, $p < 0.001$, and decreased significantly in the backward condition, $-8.53\% \pm 3.61\%$; $t(9) = -7.47$, $p < 0.001$. In the voluntary condition, saccade amplitudes tended to increase in the forward direction, $3.42\% \pm 5.18\%$; $t(9) = 2.08$, $p = 0.067$, and decreased significantly in the backward direction, $-5.69\% \pm 4.14\%$; $t(9) = -4.34$, $p = 0.002$. In the reactive condition, saccade amplitudes increased significantly in the forward direction, $9.31\% \pm 4.91\%$; $t(9) = 4.91$, $p = 0.001$, and decreased significantly in the backward condition, $-8.08\% \pm 3.65\%$; $t(9) = -7.00$, $p < 0.001$. There were no significant differences between the adaptation with the perceptual task and the reactive condition, neither in the forward, $t(9) = 2.06$, $p = 0.070$, nor in the backward condition, $t(9) = 0.37$, $p = 0.723$. However adaptation differed between the perceptual task and the voluntary condition in the forward direction, $t(9) = 4.59$, $p = 0.001$, but not in the backward direction, $t(9) = 1.64$, $p = 0.136$. Consistently, adaptation was smaller for the voluntary condition than for the reactive condition in the forward direction, $t(9) = 2.97$, $p = 0.016$, but not in the backward direction, $t(9) = 1.63$, $p = 0.137$. These results show that the task-driven adaptation significantly transferred to reactive saccades (108% and 85% in backward and forward directions), which were executed at similar latencies. Transfer to voluntary saccades was only significant in the forward direction but lower than for reactive saccades (41%). This is consistent with previous reports showing none (Deubel, 1995; Collins & Dore-Mazars, 2006) or only partial transfer (Fujita, Amagai, Minakawa, & Aoki, 2002) from reactive to voluntary saccades.

If the observers did not pay attention to the different types of trials, transfer to reactive saccades could be caused by applying the same oculomotor strategy to trials with and without the perceptual task. In this case, the transfer to reactive saccades would not represent evidence for a general change in saccade programming. To test this hypothesis, we repeated the experiment with a blocked presentation of trials with and without the perceptual task (Text S3; Figure S7). This paradigm resulted in a partial but significant transfer in the forward direction to reactive saccades (39%) but not to voluntary saccades. The backward direction did not yield a significant transfer, but we believe that this is due to a smaller backward adaptation effect in that experiment compared to previous experiments rather than the result of an asymmetry between backward and forward adaptation mechanisms. Negligence of task-relevant information increased the amount of transfer in the interleaved experiment, but at least partial transfer persisted even when task requirements (with vs. without the perceptual task) were made clear by blocking trial type instead of merely cueing the upcoming trial type.

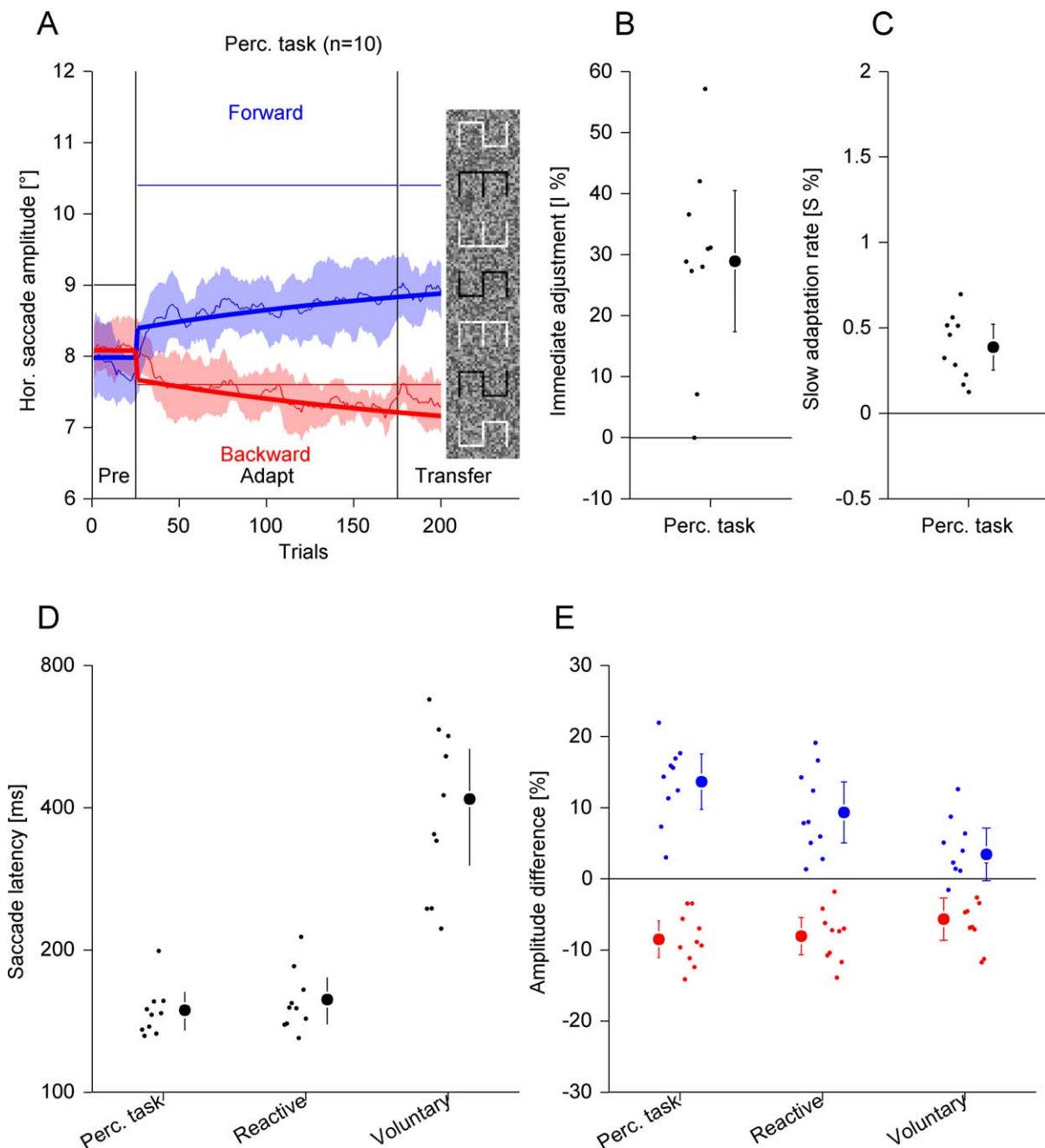


Figure 5. Experiment 6, transfer of perceptual task-driven adaptation to reactive and voluntary saccades, interleaved conditions. (A) Horizontal saccade amplitude with a perceptual task. Conventions are the same as in Figure 3A. (B) Immediate adjustment of the state-space model in the perceptual task condition. (C) Slow adaptation rate of the state-space model in the perceptual task condition. (D) Saccade latencies in the different conditions. (E) Difference in saccade amplitude in the preadaptation phase and at the end of the adaptation phase. (B–E) Small dots represent data for individual observers; large dots represent the mean across observers; error bars represent 95% confidence intervals.

Experiment with a presaccade cue (experiment 8)

In the previous experiments, the presaccade stimulus consisted of a mask of seven white characters (“8”) and the location of the discrimination character was visible only after saccade onset. It is possible that our results depended on two specific factors of the experimental

paradigm. First, the adaptation could have been caused by the transient postsaccadic cue about the location of the discrimination character. Second, the observers could have been slow to notice the postsaccadic change in discrimination location between pre-, adaptation, and post-blocks although the location of the discrimination character was held constant in a block of 100

trials and thus was perfectly predictable. To rule out these possibilities, we repeated the on-axis adaptation experiment but drew the presaccadic mask at the location of the upcoming discrimination character also in black. As a result, the location of the discrimination character was visually determined before saccade onset.

Unlike in the previous experiments, the perceptual performance did not depend on foveal acuity very much. Perceptual performance decreased only slightly from 74% correct at a retinal error of 0° to 66% correct at an error of 2.1° (Figure 2C). A linear regression did not show a negative relationship between retinal error and perceptual performance (slope -0.01 ± 0.02 , $t(8) = 1.05$, $p = 0.324$). It is possible that the presaccadic cue facilitated the segmentation of the discrimination character from the distractor characters and thus led to better perceptual performance even with large saccade errors.

The changes in amplitudes, however, were very similar to the first experiment (Figures 3D and S8). In the preadaptation phase, saccade amplitudes were similar for both directions (forward: $8.06^\circ \pm 0.55^\circ$; backward: $8.25^\circ \pm 0.38^\circ$). At the end of the adaptation phase, saccade amplitudes were increased in the forward direction ($9.14^\circ \pm 0.76^\circ$) and decreased in the backward direction ($7.52^\circ \pm 0.30^\circ$). This was supported by a significant interaction between phase and direction, $F(1, 8) = 88.77$, $p < 0.001$. Thus, the location of the discrimination character affected saccade amplitudes even when it was marked before and after the saccade. Like for the first experiment, we fitted the different models to the data. The two-parameter model had a higher relative likelihood than the one- or zero-parameter models ($76.22\% \pm 36.10\%$) (Table S1). This means that both parameters were necessary to account for the data. The two-parameter model (Figure 3E, F) revealed that $32.16\% \pm 10.77\%$ of the distance to the discrimination character was compensated by an immediate adjustment. This was significantly larger than zero, $t(8) = 9.00$, $p < 0.001$, but not significantly different from the strategic adjustment without presaccadic cue, $t(8) = 0.73$, $p = 0.485$. In every trial, $0.55\% \pm 0.48\%$ of the distance was compensated by slow adaptation. This was significantly larger than zero, $t(8) = 3.42$, $p = 0.009$, but not significantly different from the slow adjustment without presaccadic cue, $t(8) = 0.13$, $p = 0.763$.

Similar to the previous experiments, the adaptation effects were also reflected in the perceptual performance (Figure 2G). In the forward direction, performance decreased at the beginning of the adaptation from $68\% \pm 2\%$ to $61\% \pm 1\%$. At the end of the adaptation phase, it increased to $68\% \pm 2\%$, $F(2, 16) = 3.43$, $p = 0.058$. Perceptual performance in the backward direction increased during the adaptation phase: pre: $71\% \pm 1\%$; beginning: $74\% \pm 1\%$; end: 84%

$\pm 1\%$; $F(2, 16) = 16.12$, $p < 0.001$. These perceptual results were very similar to the perceptual task experiment without a presaccadic cue.

This final experiment showed that there was an adaptation effect even when the location of the discrimination character was already marked before the onset of the saccade. Hence, the adaptation was not caused by uncertainty about the location of the discrimination character or the presence of a visual transient. Because the perceptual performance did not depend on saccade error as much as in the previous experiments, it also suggests that perceptual performance might not be the crucial factor driving the adaptation.

Discussion

When observers were confronted with a perceptual task on a peripheral object, saccadic eye movements were affected by the requirements of the perceptual task, in our case, by the location of a discrimination character within the peripheral object. We found evidence that saccade targeting was changed by two processes: an immediate, presumably strategic adjustment within few trials and a slow, gradual adaptation over several dozens of trials. Over the course of 150 adaptation trials, the gradual adaptation reached a comparable magnitude as the immediate adjustment. Both processes were reflected in the amplitude and the direction of saccades. These effects were absent or significantly weaker when the observers saw the same stimuli without being engaged in the perceptual task. The important role of the perceptual task on oculomotor control was put forward previously by Montagnini and Chelazzi (2005) by showing that saccade latency and peak velocity are modified when observers aim toward locations on which a difficult perceptual task has to be performed.

There are four reasons for thinking about the task-related gradual changes in terms of saccade adaptation. First, the changes developed gradually over time, and residual effects remained after the end of adaptation, which is a hallmark of saccade adaptation (Straube, Fuchs, Usher, & Robinson, 1997). Second, the changes in saccade amplitude were comparable in magnitude to changes induced in a classical adaptation paradigm. Third, the changes in saccade direction were accompanied by changes in the saccade trajectory, which are typically observed during cross-axis adaptation of saccades (Chen-Harris et al., 2008; Schütz & Souto, 2011). Fourth, the effects transferred at least partially to reactive saccades without a perceptual task. A purely voluntary effect should not transfer to reactive saccades that are not related to the perceptual task.

This finding of a task-driven saccade adaptation has important implications for understanding the signal that drives saccade adaptation and the purpose of saccade adaptation. Comparing visual and motor signals, previous research has shown that adaptation is driven rather by visual errors than by corrective saccades (Wallman & Fuchs, 1998; Bahcall & Kowler, 2000) and that only the visual error of the saccade target matters (Madelain et al., 2010; Madelain et al., 2013). Distinguishing position errors from prediction errors, it has been shown that prediction errors have a stronger impact on adaptation than mere position errors (Bahcall & Kowler, 2000; Wong & Shelhamer, 2011; Collins & Wallman, 2012). All these studies shifted the target position during the saccade and share the common assumption that a bottom-up visual error is necessary to drive adaptation. However, in our paradigm, the position of the character array remained identical; only the designation of the discrimination character changed during the adaptation phase. This means that there were no bottom-up position or prediction errors per se. Just the top-down assignment of task relevance to the different character positions was sufficient to drive adaptation.

There are at least three possibilities for how this top-down adaptation could be achieved, and further studies are necessary to distinguish between these alternatives. First, the adaptation might be driven by the reward of seeing the discrimination character. This would be consistent with the results of a recent study showing that adaptation can be triggered merely by rewarding certain saccade amplitudes (Madelain, Paeye, & Wallman, 2011). In our case, the implicit reward by achieving a perceptual task might have been sufficient to drive saccade adaptation. Second, the perceptual task presumably also triggered a target selection process. Saccades to multiple targets or spatially extended targets typically land close to the center of gravity (Findlay, 1982; Ottes, Van Gisbergen, & Eggermont, 1984). This standard behavior was functional in our paradigm when the discrimination character was presented at the center of the peripheral array. When the character was presented at an eccentric position, global saccades were no longer functional, and the discrimination character within the array had to be targeted. Possibly this target selection process needs some learning and leads to saccade adaptation. This target selection process could already involve a presaccadic shift of attention (Kowler, Anderson, Doshier, & Blaser, 1995; Deubel & Schneider, 1996). A previous study showed that covert shifts of attention can be adapted by a spatial mismatch between the location of the cue and the target (McFadden, Khan, & Wallman, 2002). Interestingly, this adaptation of attention transferred to saccades. This leaves the possibility that the adaptation of saccades in our study

was mediated by an adaptation of attention shifts. Nevertheless, the adaptation effects must ultimately originate in the perceptual task because they were absent or significantly weaker without a perceptual task. Finally, the requirements of the perceptual task in terms of spatial acuity might have been driving adaptation. In this case, we speculate that adaptation rates should differ as a function of how much performance depends on correct foveation, i.e., spatial acuity. However, the robust adaptation effect in the experiment with a presaccadic cue at the discrimination location speaks against this possibility because then perceptual performance did not depend on the saccade error as much as in the other experiments.

The saccade landing positions in our paradigm were, in general, not particularly well tuned to the perceptual task. First, there was an undershoot of saccade amplitudes of more than 10%. This undershoot occurred although perceptual performance declined with increasing saccade error. Second, the strategic adjustment compensated for only about 20% of the distance to the discrimination character, and the gradual adaptation showed a slow learning rate of about 0.5% per trial. When taking together immediate adjustment and slow adaptation, the compensation was far from being complete. However, this does not necessarily mean that eye movements and adaptation were not optimal. First, spatial accuracy is not the only objective of the saccade system. Movement duration has to be minimized, for instance, by reducing movement amplitude, ultimately resulting in shorter interruptions of visual input (Harris, 1995). Second, the adaptation rate with the perceptual task was of the same magnitude as with the classical double-step paradigm. It is possible that we reached the upper limit of adaptation in both experiments. Third, the decline in perceptual performance with increasing saccade error was not very steep. We conjecture that a steeper decline of perceptual performance with fixation errors can lead to faster adaptation if it is driven by perceptual task demands. Hence, saccade adaptation might be a useful mechanism to optimize eye movements with respect to the execution of a perceptual task even though it did not compensate the distance to the discrimination character completely.

Task-driven adaptation has important implications for our understanding of the physiology of saccade adaptation. Single-cell studies localized subcortical saccade adaptation signals downstream of the superior colliculus (SC) (Iwamoto & Kaku, 2010; Pelisson et al., 2010). Error signals that could possibly instruct saccade adaptation have been recorded, for instance, in the oculomotor vermis of the cerebellum (Catz, Dicke, & Thier, 2008; Soetedjo, Kojima, & Fuchs, 2008; Kojima, Soetedjo, & Fuchs, 2010). Consistently, a disruption of the posterior cerebellum by transcranial magnetic

stimulation (TMS) leads to impairments in saccade adaptation (Jenkinson & Miall, 2010). Furthermore, subthreshold microstimulation in the SC induces saccade adaptation just like the peri-saccadic displacement of the saccade target (Kaku, Yoshida, & Iwamoto, 2009; Soetedjo, Fuchs, & Kojima, 2009). Such subcortical and especially cerebellar foundations of saccade adaptation emphasize the low-level purpose of saccade adaptation to correct for fluctuations in the oculomotor system function (Albert et al., 2012). This view is challenged by recent functional magnetic resonance imaging and TMS studies, which found evidence for cortical contributions to saccade adaptation (Gerardin, Miquee, Urquizar, & Pelisson, 2012; Panouilleres et al., 2012). Interestingly, different neural structures were activated for reactive and voluntary saccades: the middle-temporal and temporo-parietal areas for reactive saccades and parietal areas for voluntary saccades. Frontal areas and the cerebellum were activated for both saccade types. These cortical foundations of saccade adaptation can be interpreted as evidence that saccade adaptation is not just a low-level mechanism. This view is also supported by the finding that saccade adaptation occurs in spatiotopic rather than retinotopic coordinates (Zimmermann, Burr, & Morrone, 2011). Our results show that a top-down error signal can drive saccade adaptation as well. This signal could originate in the middle-temporal and temporo-parietal areas because these are specifically modulated during adaptation of reactive saccades (Gerardin et al., 2012). However, it could also originate in the SC, given its important role for guiding attention (Zenon & Krauzlis, 2012) and eye movements (Robinson, 1972).

The field of active vision has shown that vision is modulated by eye movements (Ross, Morrone, Goldberg, & Burr, 2001; Schütz et al., 2011) and has demonstrated the need to study visual perception under natural conditions, in which the eyes are rarely stationary. Consequently, the question of how saccade adaptation affects the perceived location of visual objects has been studied in great detail (Pelisson et al., 2010): Adaptation of saccades leads to a distortion of perceived locations, both before saccade execution (Awater, Burr, Lappe, Morrone, & Goldberg, 2005) and during steady fixation (Zimmermann & Lappe, 2010). Because our perceptual task only involved the discrimination of characters, we do not know whether perceived location was also affected by adaptation in our data.

The effects of perception on eye movements, however, have received less attention. Most of our knowledge about basic oculomotor functioning comes from studies using simple targets, which are perceptually irrelevant. Our results illustrate that even a seemingly basic oculomotor process, such as saccade

adaptation, can be influenced by high-level perceptual requirements. This means that oculomotor functioning is best studied in natural situations in which observers are engaged in a perceptual or behavioral task.

Keywords: motor adaptation, eye movements, visual perception

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