RESEARCH ARTICLE

Adaptation of catch-up saccades during the initiation of smooth pursuit eye movements

Alexander C. Schütz · David Souto

Abstract Reduction of retinal speed and alignment of the line of sight are believed to be the respective primary functions of smooth pursuit and saccadic eye movements. As the eye muscles strength can change in the short-term, continuous adjustments of motor signals are required to achieve constant accuracy. While adaptation of saccade amplitude to systematic position errors has been extensively studied, we know less about the adaptive response to position errors during smooth pursuit initiation, when target motion has to be taken into account to program saccades, and when position errors at the saccade endpoint could also be corrected by increasing pursuit velocity. To study short-term adaptation (250 adaptation trials) of tracking eye movements, we introduced a position error during the first catch-up saccade made during the initiation of smooth pursuit—in a ramp-step-ramp paradigm. The target position was either shifted in the direction of the horizontally moving target (forward step), against it (backward step) or orthogonally to it (vertical step). Results indicate adaptation of catch-up saccade amplitude to back and forward steps. With vertical steps, saccades became oblique, by an inflexion of the early or late saccade trajectory. With a similar time course, post-saccadic pursuit velocity was increased in the step direction, adding further evidence that under some conditions pursuit and saccades can act synergistically to reduce position errors.

Keywords Saccade adaptation ·
Pursuit adaptation · Saccadic eye movements ·
Smooth pursuit eye movements · Catch-up saccade

Introduction

Primates use primarily smooth pursuit eye movements (hence *pursuit*) to reduce objects of interest's retinal speed and saccadic eye movements to keep them centred onto the fovea. Accordingly, it was originally thought that saccadic and smooth pursuit eye movements require completely distinct visual inputs: saccades correct retinal position error, while pursuit eye movements correct retinal velocity error (Rashbass 1961).

However, there is now strong evidence that saccades take also into account the velocity of the target. For instance, saccades made to moving targets (in particular the first catch-up saccades) are adjusted in proportion of target speed to compensate for the displacement of the target during the temporal interval between programming and execution (Gellman and Carl 1991; Guan et al. 2005; Kim et al. 1997). If saccade programming was uniquely based on the target position sampled 100 ms before saccade onset, we should expect a strong undershoot—about 1° for a target moving at a moderate speed of 10 deg/s. Moreover, the frequency of catch-up saccades during maintained pursuit is best predicted by a measure combining retinal slip and position error, namely the time it would take the eye to cross the target if maintaining the same velocity (de Brouwer et al. 2002b).

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Although growing evidence indicates that the pursuit system is sensitive to target position, it is still a matter of debate whether this sensitivity results from the orienting of attention to a localized transient (Blohm et al. 2005), from apparent motion (Carl and Gellman 1987), or the incorporation of a position signal per se. The ability of a position error to drive pursuit and saccadic adaptation would provide an independent source of evidence for the availability of a position signal to both oculomotor systems.

In daily life, the precision of saccadic and pursuit eye movements has to be maintained although the strength of the eye muscles is continuously changing, due to fatigue, growth, injury, or disease (Optican et al. 1985). Therefore, control systems have to adapt to these changes. In the laboratory, saccadic adaptation is usually investigated with the double step-paradigm, in which the target is shifted during the saccade. As a result of this intra-saccadic target step, saccades become dysmetric and corrective saccades are performed. The repeated application of such a target step causes saccade gain to adapt gradually to the new target position until saccades land eventually on target.

Pursuit gain can be adapted in a similar way to saccade gain, by applying predictable velocity changes to the pursuit target (Fukushima et al. 1996; Kahlon and Lisberger 1996; Nagao and Kitazawa 1998; Ogawa and Fujita 1997). Adaptation of pursuit gain has been shown in the open-loop (Kahlon and Lisberger 1996) and during the closed-loop period (Fukushima et al. 1996). Furthermore, when target velocity is changed during the first catch-up saccade, both saccade and pursuit gain can be adapted at the same time (Nagao and Kitazawa 1998; but see Ogawa and Fujita 1997), adding evidence that velocity is an input to the saccadic system.

In the present study, we investigated the effects of a target step that is applied during the first catch-up saccade during pursuit initiation. We asked if such a position signal can elicit adaptation of saccade amplitude, pursuit velocity, or both. In particular, we wondered wether saccade adaptation can be reliably obtained during pursuit initiation. Under these conditions, a generalization across saccade amplitude is required, because the amplitude of catch-up saccades varies with their latency. Moreover, it could be that a position signal is obliterated by subsequent motion, thereby reducing saccade adaptation.

In accordance with recent proposals that there is a position and velocity input into the pursuit system (Blohm et al. 2005; Orban de Xivry et al. 2006, 2008), we expect that both oculomotor systems show coordinated sensory-motor plasticity induced by a systematic position error. During pursuit initiation, adaptation to systematic position errors can be done by modifying different parameters other than saccade amplitude, like pursuit velocity after or before the saccade, or the overall pursuit visuomotor gain. The

position error can also be corrected by secondary saccades (Hallett 1978). However, a correction by secondary saccades has two disadvantages compared to a change in pursuit velocity: first the position error will be corrected with a longer latency and second, vision will be suppressed during the secondary saccade.

To anticipate the results, we show that for target steps in the direction of the pursuit eye movement there is a robust adaptation of the amplitude of catch-up saccades. Pursuit adaptive changes were too small to raise above measurement noise in that paradigm. However, when adapting to steps in the vertical direction (orthogonal to the direction of movement), we show that saccades become oblique and post-saccadic pursuit increases substantially in the vertical direction by up to 1–2 deg/s, contributing to the reduction of the post-saccadic position error.

Materials and methods

Subjects

The first experiment was performed by the authors and seven naïve subjects; the second by the authors and six naïve subjects, of 22–29 years old. Data from five subjects in the first experiment and four subjects in the second experiment were collected in Geneva, the rest of the data were collected in Gießen with the same display and eye-tracker. The experiments were done in compliance with the ethical regulations of the University of Geneva and of the University of Gießen.

Equipment

Subjects had their head on a chinrest 46 cm away from a 37-cm wide CRT screen (ELO Touchsystems, Fremont, CA, USA), with a 100 Hz refresh rate. Stimulus presentation was controlled by a custom-made routine that used the SDL C library (http://www.libsdl.org/). Data analysis was performed with MATLAB (The Mathworks, Inc.).

Visual stimuli

The time course of a trial in Experiment 1 and 2 is shown in Fig. 1. At trial start, a black ring (0 cd/m^2; $0.1° \times 0.1°$) was displayed over a middle-gray background (30 cd/m^2). When the subject pressed a button to start the trial, the ring turned red (3 cd/m^2) and started to move after a random foreperiod of 0.5–1 s. The first catch-up saccade of a latency of more than 100 ms was detected online. Saccades with latencies below 100 ms were ignored. In an adaptation trial, the detection of the first catch-up saccade triggered a step of the pursuit target. The step was applied during
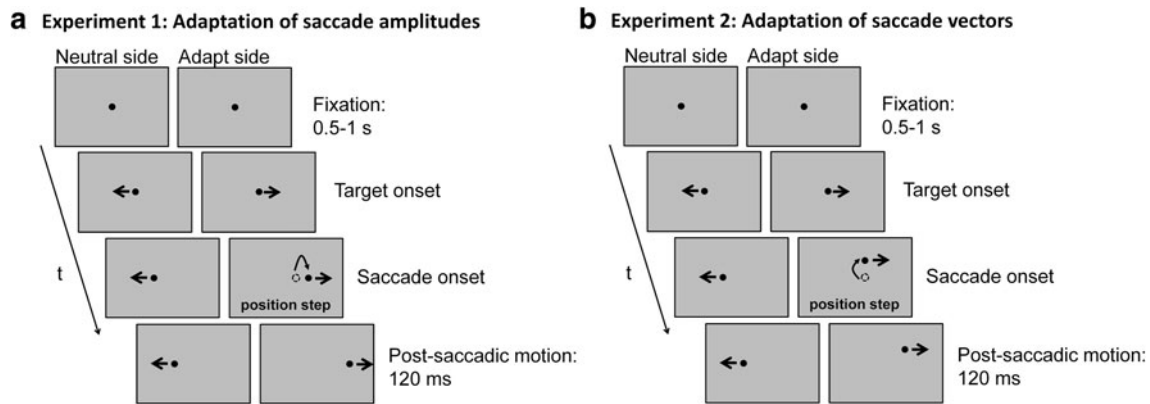
a Experiment 1: Adaptation of saccade amplitudes

b Experiment 2: Adaptation of saccade vectors

Fig. 1 Trial time course. **a** Experiment 1: the target steps during the first saccade when it moves in the rightward direction (the *adaptation side*). After the saccade offset, the target moves further for 120 ms in the leftward (the *neutral side*) or rightward direction. **b** Experiment 2: the target steps vertically, orthogonally to the direction of target motion, to test adaptation of saccade direction

saccade mid-flight due to the delay in accessing the eye-tracker recordings and to a larger extent to the refresh frequency of the visual display, of one frame every 10 ms. In all trials, the pursuit target disappeared 120 ms after the first catch-up saccade had been detected. Rapid extinction of the target had the purpose of reducing the number of corrective saccades, while still optimizing adaptation effects, as saccadic adaptation does not benefit from presenting the stimulus for more than 100 ms after the saccade offset (Hopp and Fuchs 2004).

Eye movement recording and analysis

Vertical and horizontal eye movements were recorded by a head-mounted, video-based eye-tracker (EyeLink II, Osgoode, Ontario) with a sampling rate of 500 Hz (250 Hz in one session). The position noise is specified to be of 0.01 RMS and the velocity noise of 0.5 deg/s RMS (EyeLink II User Manual). Eye velocity was obtained by digital differentiation. As we wanted to measure pre- and post-saccadic pursuit velocity close to the onset and offset of saccades, we did not filter the position or velocity traces, because any filtering could potentially contaminate the pursuit response with a saccade component.

Saccades were detected online by using a 20 deg/s velocity criterion. However, for offline analysis, we used the default EyeLink II saccade detection algorithm to set saccade onsets and offsets. This algorithm uses a velocity threshold of 22 deg/s to which the average velocity over the last 40 ms is added (which is often a negligible correction before the first catch-up saccade), and an acceleration threshold of 8,000 deg/s². Saccade amplitude was defined as the distance between the end point and the start point of the saccade. Offline, we excluded trials in which the first saccade did not occur between 100 and 400 ms after target onset (<3% in Experiment 1 and <2% in

Experiment 2) or if the gain of the first saccade was less than 0.2 (<1% in Experiment 1).

For statistical analysis, we averaged post-saccadic pursuit velocity within an interval of 30–60 ms after the end of the saccade (Lisberger 1998). Results were qualitatively similar with an interval of 40–70 ms. Pre-saccadic pursuit was averaged within 40–10 ms before the onset of the saccade. As catch-up saccades contain a pursuit component (de Brouwer et al. 2002a), we removed this component to get a pure measure of saccadic amplitude. Following de Brouwer et al. (2002a), the uncontaminated saccade amplitude ($S_{amp-corr}$) was calculated according to Eq. 1: the pursuit component is estimated by multiplying the average of the pre- and post-saccadic pursuit velocity (PV_{pre}, PV_{post}, in deg/s) by the duration of the saccade (S_{dur}, in seconds). The pursuit component is then subtracted from the observed saccade amplitude (S_{amp}).

$$S_{amp-corr} = S_{amp} - \left[\left(PV_{pre} + PV_{post} \right)/2 \right] * S_{dur} \qquad (1)$$

In Experiment 2, saccade slopes were defined as the ratio of vertical and horizontal saccade amplitude (Eq. 2). To get a pursuit-free estimation of the saccade vector, we also used the corrected saccade amplitude for this analysis.
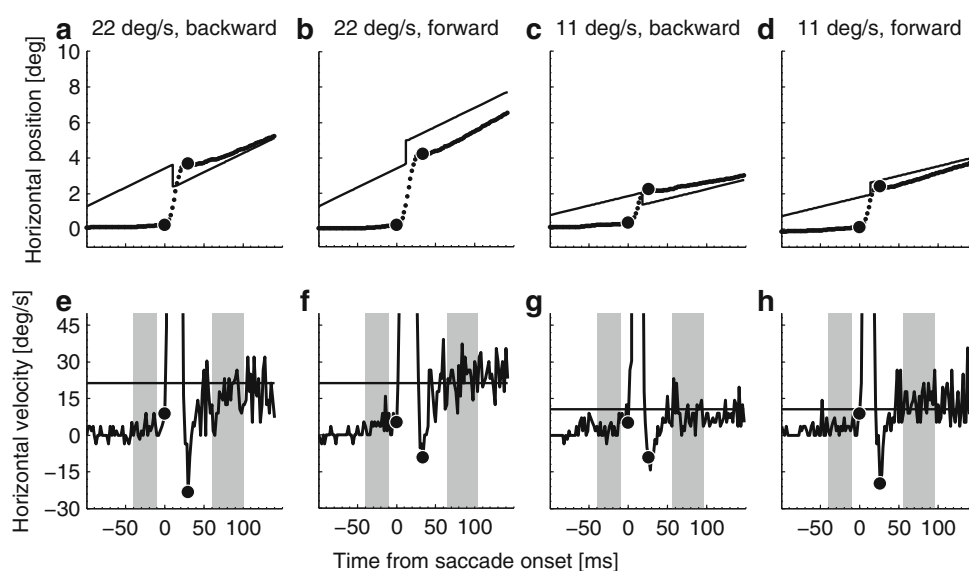
$$S_{slope-corr} = S_{amp-corr-v}/S_{amp-corr-h} \qquad (2)$$

As saccades can become curved during vector adaptation (Chen-Harris et al. 2008), we also calculated the early and late slope separately. First we split the saccades in two halves based on the (corrected) horizontal amplitude. Then, we calculated the slope according to Eq. 2 for the two halves separately.

Adaptation procedure

Subjects were asked to pursue a moving target, which direction (leftward or rightward) was randomized. In 100

Fig. 2 Experiment 1: sample traces with two ramp speeds, backward and forward steps. **a**, **b**, **e**, **f** 22 deg/s ramp speed. **c**, **d**, **g**, **h** 11 deg/s ramp speed. **a**, **c**, **e**, **g** Backward step. **b**, **d**, **f**, **h** Forward step. Saccade on and offsets are marked by *large dots*. **a–d** Eye and target position. **e–h** Eye and target velocity. The *gray shaded areas* represent the time intervals over which we averaged pre- and post-saccadic pursuit velocity. Single eye movement traces whose saccade amplitude is close to the mean amplitude in the adaptation phase are shown

pre-adaptation trials, the target trajectory was the same for both directions. In the following 400 adaptation-phase trials, rightward-moving targets (adaptation direction) stepped during the first catch-up saccade, while in mid-flight. There was no step for leftward-moving targets (neutral direction). The adaptation phase was followed by 100 post-adaptation trials identical to pre-adaptation trials. Trials were self-paced, by pressing a key on a game pad. The inter-trial interval was on average 3.72 s (SD 0.97 s). Within this time-scale, adaptation changes can be presumed to result essentially from a fast adaptation process. Saccade adaptation results from the interplay between a slow and fast adaptation process (Ethier et al. 2008). The fast process has a memory that is an order of magnitude shorter than the memory of the slow process, estimated to be respectively of about 30 and 500 s by Ethier et al. (2008). The fast process is also an order of magnitude more sensitive than the slow process to error signals.

Experiment 1: adaptation of saccade amplitude

In the first experiment, we changed the horizontal position of the eye movement target after the first saccade after target motion onset was detected (cf. Fig. 1a). We tested four different conditions: we used either a fast speed (22 deg/s, Fig. 2a, b) or a slow speed (11 deg/s, Fig. 2c, d) and we shifted the target either opposite to the direction of motion (backward condition, Fig. 2a, c) or in the same direction (forward condition, Fig. 2b, d). All subjects performed all four conditions in the following order: 22 deg/s, backward; 22 deg/s, forward; 11 deg/s, backward; 11 deg/s, forward. There were at least 24 h between two consecutive sessions. A backward shift was expected to lead to a reduction of saccade amplitude and pursuit speed, whereas a forward shift should

lead to an increase in saccade amplitude and pursuit speed. The magnitude of the step (St) was calculated according to Eq. 3, which takes into account the target velocity (v in deg/s) and the saccade latency (sl in seconds), starting from the onset of target motion. We shifted the target position by 25% of the predicted target eccentricity at the end of the saccade, assuming the average saccade duration would be 50 ms, which overestimated the actual saccade duration, resulting in a larger step size than we first planned.

$$St = v * (sl + 0.05) * 0.25 \tag{3}$$

Experiment 2: adaptation of saccade vector

In the adaptation phase of the second experiment, we shifted the vertical position of the horizontally moving target upwards, as shown in Figs. 1b and 3. We tested two different step sizes, corresponding to 25% (Fig. 3a, c, e) and 50% (Fig. 3b, d, f) of the estimated horizontal saccade amplitude necessary to land on target (effectively 32 and 63% of the corrected saccade amplitude, respectively, see below), with only 11 deg/s speed. All subjects performed first the small step and then the large step condition, at least 24 h apart.

Control of manipulation

To make sure that our manipulation worked as intended, we analyzed the timing of the target steps. On average the step occurred 15.1 ms (SD 3.4) after the saccade onset. The average saccade duration was 36.3 ms (SD 6.6) with the 22 deg/s speed and 28.5 ms (SD 5.9) with the 11 deg/s speed. Hence, the step occurred in saccade mid-flight. Furthermore, the average step latency and the average actual saccade onset had a near perfect correlation (rho = 0.98, $P < 0.001$), which indicates that we reliably

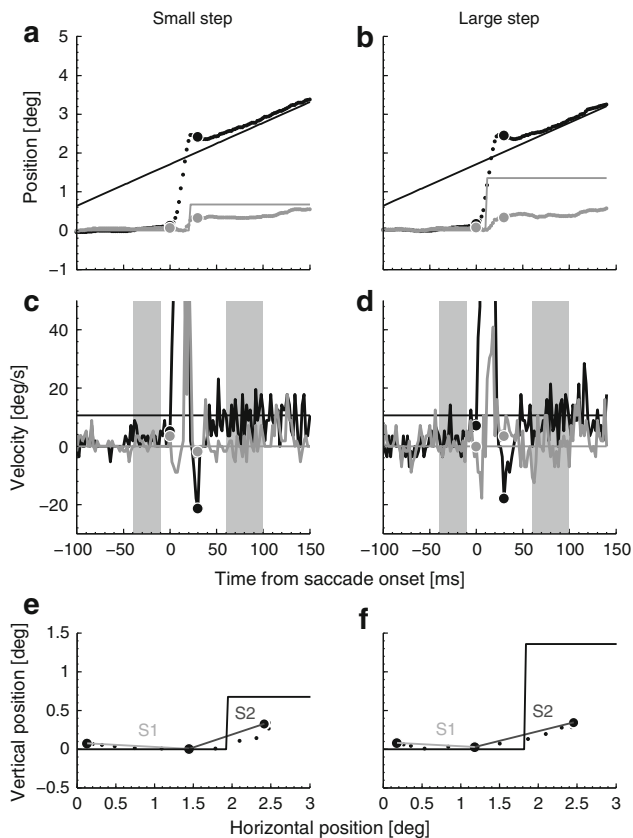**Fig. 3** Experiment 2: sample traces with two step sizes. **a**, **c**, **e** Small step condition. **b**, **d**, **f** Large step condition. **a**, **b** Horizontal (*black*) and vertical position (*gray*) are plotted over time. Saccade on and offsets are marked by *large dots*. **c**, **d** Horizontal (*black*) and vertical velocity (*gray*) are plotted over time. Saccade on and offsets are marked by *large dots*. **e**, **f** Vertical position is plotted over horizontal position for the duration of the saccade. The start saccade slope (S1) is indicated by the *light gray line* and the end slope (S2) by the *dark gray line*. *Large dots* indicate the start, mid-point, and end of the saccade. Single eye movement traces whose saccade slope is close to the mean slope in the adaptation phase are shown

applied the step at the same time relative to saccade onset. This is also supported by the fact that we did not find any correlation between the saccade latency and the latency of the step relative to saccade onset (rho = −0.01, P = 0.630). The average step size amounted to 1.32 deg (SD 0.10) with the 22 deg/s speed and to 0.68 deg (SD 0.05) with the 11 deg/s speed. We estimated the step size based on the saccade latency and an estimated saccade duration of 50 ms (Eq. 3). However, the average saccade duration was smaller. Hence, the actual step size relative to the measured saccade amplitude was of about 35% instead of 25% for both speeds. The same pattern was observed in Experiment 2.

Statistical testing

For statistical testing, we averaged data across the pre-adaptation trials (T1), the last 100 adaptation-phase trials

(T2) and the post-adaptation trials (T3). In the first experiment, we ran a repeated-measures ANOVA for forward and backward adaptation separately, because the two can be considered as distinct processes. We tested the factors direction (adaptation and neutral), speed (11 and 22 deg/s), and time (T1, T2, and T3). In the second experiment, we ran a repeated-measures ANOVA with the factors direction (adaptation and neutral), step size (small and large), and time (T1, T2, and T3). In this design, an effect of adaptation would result in a significant interaction between the factors direction and time. To compare further between levels, we ran one-sided, paired *t*-tests. A bonferroni correction was applied for multiple testing. For graphical illustration, the data from each phase were averaged across subjects by using a running average with a 20-trial window (about 10 trials in the adaptation direction), as shown in Figs. 4 and 6.

Results

Experiment 1: adaptation of saccade amplitude

In the first experiment, we attempted to adapt the amplitude of the first catch-up saccade made during smooth pursuit initiation. In order to do so, we shifted the position of the moving target after the first catch-up saccade started. We tested four different experimental conditions: a slow (11 deg/s) and a fast target speed (22 deg/s) were combined with a step in the direction of target motion (forward adaptation) and opposite to it (backward adaptation). We expected backward adaptation to lead to a shortening of saccade amplitude, and forward adaptation to lead to a lengthening of amplitude, compensating for the position error. We expected adaptation effects (in saccade amplitude and in pursuit velocity) to be similar in proportion for both target speeds.

In all four conditions, we found changes in saccade amplitude in the adaptation direction that were consistent with the predictions (Fig. 4a, b) when we compare average adaptation direction values in the pre-adaptation trials (T1) with the last 100 adaptation-phase trials (T2) and the post-adaptation trials (T3). Backward adaptation led to a reduction of saccade amplitude by 15% (T1 vs. T2) with the slow speed [T1: 2.01 (SE 0.18); T2: 1.71 (SE 0.13); T3: 1.81 deg (SE 0.12)] and 12% with the fast speed [T1: 3.59 (SE 0.21); T2: 3.16 (SE 0.19); T3: 3.47 deg (SE 0.24)]. Forward adaptation led to an increase in saccade amplitude by 13% with the slow speed [T1: 1.94 (SE 0.12); T2: 2.20 (SE 0.15); T3: 2.05 deg (SE 0.13)] and 11% with the fast speed [T1: 3.57 (SE 0.18); T2: 3.98 (SE 0.23); T3: 3.73 deg (SE 0.22)]. Importantly, the amplitude did not return to the pre-adaptation state during the post-adaptation
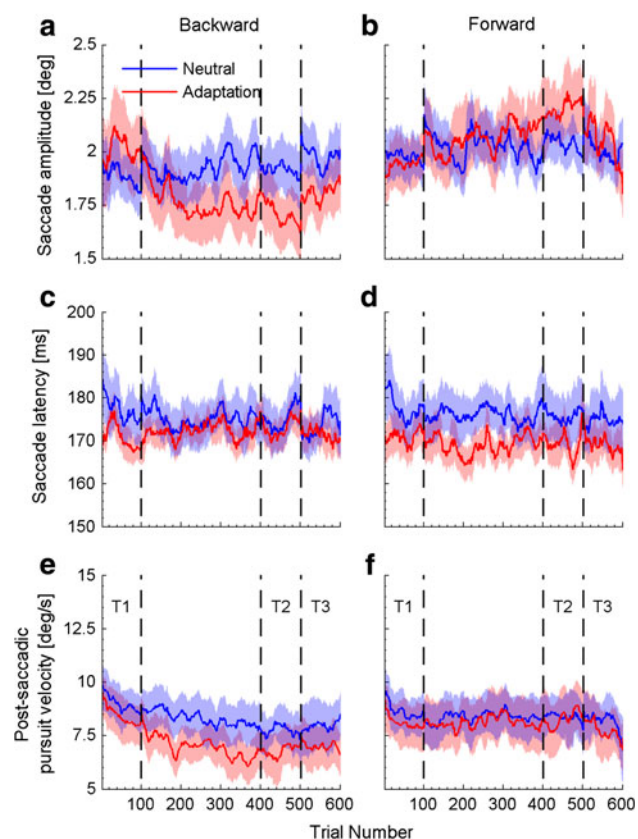
Fig. 4 Experiment 1: time course of saccade amplitude adaptation. **a**, **b** Saccade amplitude. **c**, **d** Saccade latency. **e**, **f** Post-saccadic pursuit velocity. **a**, **c**, **e** Backward step. **b**, **d**, **f** Forward step. The neutral direction is shown in *blue* and the adaptation direction in *red*. The mean across subjects and the standard error of the mean (*the shaded area*) are shown. *The dashed vertical lines* separate the trials in the pre-adaptation (T1), late-adaptation (T2), and post-adaptation (T3) phase. Only data for the 11 deg/s ramp speed are shown

phase (T3). This gives an indication that the observed effects resulted from neural plasticity and not from strategic behavior.

With backward steps, the ANOVA confirmed a significant main effect of speed ($F_{(1,8)} = 349.83$, $P < 0.001$), time ($F_{(2,16)} = 8.12$, $P = 0.004$), and a significant interaction between time and direction ($F_{(2,16)} = 23.07$, $P < 0.001$). A significant effect of speed on saccade amplitude is expected as a logical consequence of more eccentric targets with the fastest ramp. As speed did not interact with direction or time, we averaged across ramp speeds for the post hoc tests, showing a significant difference in the adaptation direction between T1 and T2 ($t(8) = 5.47$, $P = 0.001$) and between T1 and T3 ($t(8) = 2.64$, $P = 0.030$). Hence, the saccade amplitude was significantly reduced by our manipulation and this effect persisted even when the manipulation was stopped. For forward adaptation, there was also a significant main effect of speed ($F_{(1,8)} = 218.95$, $P < 0.001$), time

($F_{(2,16)} = 11.06$, $P = 0.001$), and again a significant interaction between direction and time ($F_{(2,16)} = 10.64$, $P = 0.001$), indicating the influence of the manipulation over time. Post hoc tests resulted in a significant difference in the adaptation direction between T1 and T2 ($t(8) = 6.35$, $P < 0.001$) and a marginally significant difference between T1 and T3 ($t(8) = 2.17$, $P = 0.061$). In sum, saccade amplitude was significantly adapted by our manipulation and this effect persisted during post-adaptation trials.

As we used the saccade latency to predict the amplitude of the saccade (see Eq. 3), which was in turn used to determine the appropriate step size, the stability of saccade latencies is crucial for our paradigm. Average saccade latencies ranged from 160 to 173 ms between conditions and adaptation phases. The average difference between saccade latencies in the pre-adaptation trials (T1) and the last 100 adaptation trials (T2) was below 3% in all conditions, as shown in Fig. 4c, d, and therefore can be considered as a negligible factor in explaining away modifications of saccade amplitude elicited by the manipulation.

The initial pursuit response after the saccade offset does not take into account the visual consequences of the saccade, as it takes about 100 ms to close the visuo-motor loop (Lisberger et al. 1987). Therefore, post-saccadic velocity, in the same way as saccade amplitude, might be adapted after several trials. To test for an effect of the steps on post-saccadic pursuit, we averaged pursuit velocity from 30 to 60 ms after saccade offset (Fig. 5b, d). Similar to saccade amplitude, we expected the velocity of post-saccadic pursuit to decrease during backward adaptation and increase during forward adaptation. The differences in pursuit velocity between T1, T2, and T3 were consistent with the prediction, but were small in magnitude compared to the variability in the measure, as shown in Fig. 4e, f. For backward adaptation, velocity was 6% smaller at the end of adaptation with the fast speed [T1: 12.91 deg/s (SE 1.66); T2: 12.15 deg/s (SE 1.72); T3: 12.51 deg/s (SE 1.86)] and 19% smaller with the slow speed [T1: 8.46 deg/s (SE 0.98); T2: 6.82 deg/s (SE 0.99); T3: 7.01 deg/s (SE 1.01)]. For forward adaptation, pursuit velocity did not increase substantially neither with the fast speed [T1: 12.96 deg/s (SE 1.61); T2: 13.07 deg/s (SE 2.27); T3: 13.65 (SE 2.04)] nor with the slow speed [T1: 8.14 (SE 1.02); T2: 8.28 (SE 1.25); T3: 7.75 deg/s (SE 1.13)].

For backward adaptation, an ANOVA on post-saccadic pursuit velocity revealed a significant main effect of speed ($F_{(1,8)} = 56.94$, $P < 0.001$) and time ($F_{(2,16)} = 4.00$, $P = 0.039$). There was a significant interaction between speed and time ($F_{(2,16)} = 6.14$, $P = 0.011$) but not between direction and time ($F_{(2,16)} = 2.09$, $P = 0.157$). For the forward adaptation condition, there was only a significant main effect of speed ($F_{(1,8)} = 59.22$,
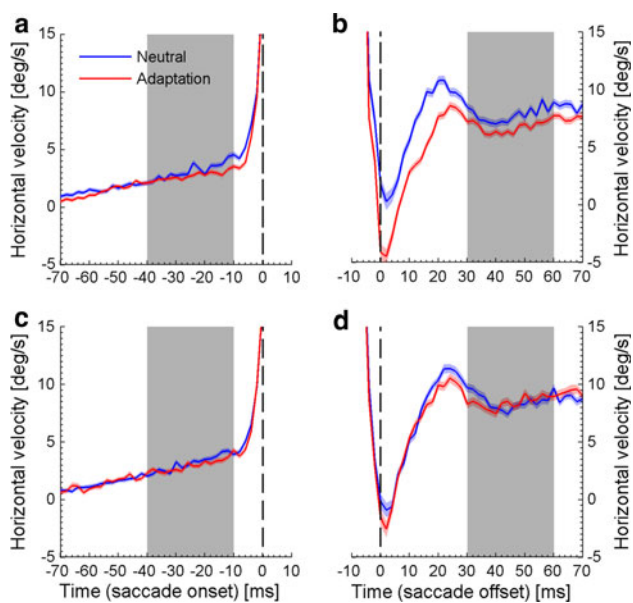
Fig. 5 Experiment 1: mean eye velocity traces in the last 100 adaptation trials (T2) across subjects. **a**, **b** Backward step. **c**, **d** Forward step. **a**, **c** Eye velocity before the first catch-up saccade, aligned to the onset of the saccade (*dashed line*). **b**, **d** eye velocity after the first catch-up saccade, aligned to the offset of the saccade (*dashed line*). The neutral direction is shown in *blue* and the adaptation direction in *red*. The shaded area is bounded by the standard error of the mean. *The gray shaded areas* represent the time intervals over which we averaged pre- and post-saccadic pursuit velocity. Only data for the 11 deg/s ramp speed are shown

$P < 0.001$). In sum, consistently with the small effect sizes for forward and backward adaptation, the statistical analysis shows no significant adaptation effects of post-saccadic pursuit velocity.

Pursuit onset precedes most often the onset of the first saccade (Kimmig et al. 2002). It might be that pre-saccadic pursuit is adapted by the intra-saccadic target step (Ogawa and Fujita 1997), influencing the amplitude of the first catch-up saccade. Pre-saccadic pursuit velocity, as measured from 40 to 10 ms before the onset of the first catch-up saccade (Fig. 5a, c), ranged from 2.74 to 3.71 deg/s between conditions and adaptation phases and was lower by about 13% in the last 100 adaptation trials (T2) compared to pre-adaptation trials (T1) with the two ramp speeds. In the backward condition, there was a significant main effect for time ($F(2,16) = 4.72$, $P = 0.025$) and a significant three-way interaction between direction, time, and speed ($F(2,16) = 4.00$, $P = 0.039$). A significant three-way interaction could indicate an adaptation effect depending on ramp speeds, but post hoc tests revealed no significant difference (comparing T1 vs. T2 in the adaptation direction, with the slow or fast speed) that would indicate an adaptation effect. In the forward condition, only the main effect of time was significant ($F(2,16) = 5.54$, $P = 0.015$), indicating an unspecific reduction of pre-

saccadic pursuit velocity over time, but no adaptation effect.

In summary, while our manipulation was successful in adapting the amplitude of the first catch-up saccade during pursuit, we found little evidence for adaptation of post-saccadic pursuit, pre-saccadic pursuit, or saccade latency.

Experiment 2: adaptation of saccade vector

The results of Experiment 1 were inconclusive about the effects of a position error on pursuit adaptation. While we found a reliable saccade adaptation in all four conditions, there was little sign of adaptation of post-saccadic pursuit velocity. As the target steps were rather small and along the same dimension as the pursuit, effects might have been concealed by the large variability of post-saccadic pursuit. To clarify this issue, we attempted to adapt the saccade vector instead of the saccade amplitude in a second experiment. We only tested the slow speed (11 deg/s) and applied either a small (25% of the predicted horizontal saccade amplitude, effectively 32% of the corrected saccade amplitude) or a large (50%, effectively 63%) upward step, i.e., orthogonally to the horizontal target motion. On average, the small step was of 0.68 deg (SD 0.06) and the large step was of 1.38 deg (SD 0.1).

To quantify the effect of the orthogonal target step on the trajectory of the first catch-up saccade (Fig. 3), we calculated the saccade *slope* as the ratio of vertical and horizontal (corrected) saccade amplitude (Eq. 2). This ratio is zero for horizontal saccades and is positive for oblique saccades in the adaptation direction. We compared again average values between pre-adaptation (T1), end of adaptation (T2), and post-adaptation (T3) trials (see Fig. 6a, b). Saccade slope increased during adaptation in the small step condition [T1: 0 (SE 0.01); T2: 0.15 (SE 0.04); T3: 0.06 (SE 0.02)] and the large step condition [T1: 0.01 (SE 0.03); T2: 0.25 (SE 0.04); T3: 0.09 (SE 0.02)]. An ANOVA showed that all main effects were significant: direction ($F(1,7) = 23.52$, $P = 0.002$), step size ($F(1,7) = 12.92$, $P = 0.009$), and time ($F(2,14) = 26.56$, $P < 0.001$). There were also significant interactions between direction and step size ($F(1,7) = 8.47$, $P = 0.023$), step size and time ($F(2,14) = 5.04$, $P = 0.023$) and most importantly between direction and time ($F(2,14) = 25.31$, $P < 0.001$). The three-way interaction was also significant ($F(2,14) = 6.36$, $P = 0.011$), which could indicate larger adaptation effects with the large step, which is apparent in Fig. 6a, b. Post hoc tests showed that the saccade slope in the adaptation direction differed significantly between T1 and T2 for both step sizes (small step: $t(7) = 4.53$, $P = 0.005$; large step: $t(7) = 7.37$, $P < 0.001$) and between T1 and T3 (small step: $t(7) = 3.24$, $P = 0.028$; large step: $t(7) = 5.70$, $P = 0.001$). This indicates that our
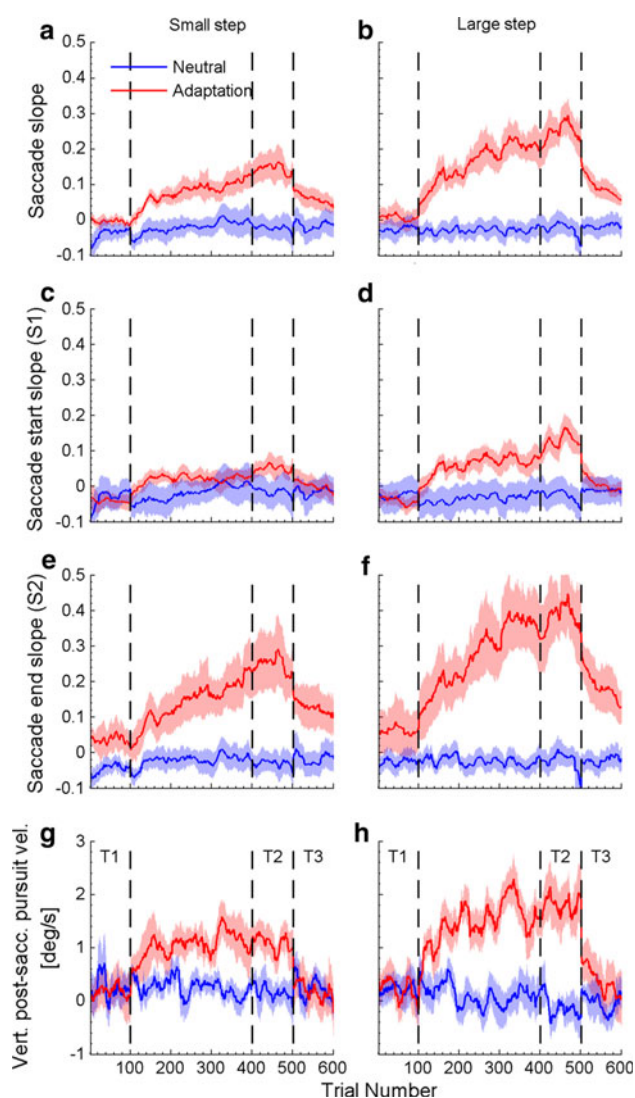
Fig. 6 Experiment 2: time course of adaptation of the saccade vector. **a, b** Saccade slope. **c d** Saccade start slope. **e, f** Saccade end slope. **g, h** Vertical post-saccadic pursuit velocity. **a, c, e, g** Small step. **b, d, f, h** Large step. Conventions are the same as in Fig. 4

manipulation successfully altered the vector of the initial catch-up saccade and that this effect was still present after the end of adaptation, indicating a gradual return to the pre-adaptation state.

We also tested whether the orthogonal adaptation procedure affected the horizontal amplitude of the catch-up saccades. The average horizontal saccade amplitude ranged from 2.11 to 2.18, and increased by 1% between T1 and T2 in the adaptation direction. An ANOVA on horizontal saccade amplitude showed no significant effect.

Recently, it has been shown that saccades become curved in oblique adaptation paradigms (Chen-Harris et al. 2008). The authors argued that the curvature reflects two different adaptation mechanisms with different time scales: the slow changing mechanism affects the initial trajectory

of the saccade and the fast changing mechanism controls the late trajectory. To test which of these mechanisms was modified by our manipulation, we split each saccade trajectory in two halves and calculated the ratio of vertical and horizontal amplitudes separately for each of the two halves. Figure 6c–f shows that adaptation of the late slope (S2) was more important than of the early slope (S1), with no clear difference in time course. At the end of the adaptation phase, S1 was 0.05 (SE 0.02) with the small step—equivalent to 2.9 deg inclination—and 0.13 (SE 0.03) with the large step—equivalent to 7.4 deg inclination. S2 was 0.25 (SE 0.08) with the small step, or 14 deg, and 0.38 (SE 0.09) with the large step, or 21 deg. Thus, subjects compensated for the orthogonal target step mainly in the second part of the saccade trajectory.

To test statistically differences in adaptation between the early and late saccade trajectory, we computed a repeated-measures ANOVA with the factors step size, time, and saccade trajectory (S1, S2) only for trials in the adaptation direction. We obtained significant main effects of step size ($F(1,7) = 13.09$, $P = 0.009$) and time ($F(2,14) = 28.13$, $P < 0.001$). There was also a significant interaction between time and trajectory ($F(2,14) = 8.96$, $P = 0.003$), which could indicate a stronger effect of the manipulation on the late saccade trajectory. The interaction between step size and time was also significant ($F(2,14) = 7.33$, $P = 0.007$), which may indicate a larger effect of adaptation with the large step (Fig. 6c–f). However, post hoc tests showed no significant difference between S1 and S2, either in T2 or in T3.

Like in the first experiment, we analyzed the influence of the target step on post-saccadic pursuit velocity. As the step was orthogonal to the target trajectory, we first considered vertical pursuit velocity in further analysis (30–60 ms interval). As shown in Figs. 6g, h and 7b, vertical pursuit velocity increased during the adaptation phase in the small step condition [T1: 0.18 (SE 0.32); T2: 1.11 (SE 0.23); T3: 0.20 deg/s (SE 0.34)] and in the large step condition [T1: 0.24 (SE 0.30); T2: 1.82 (SE 0.40); T3: 0.39 deg/s (SE 0.39)]. The ANOVA showed a significant main effect for time ($F(2,14) = 18.68$, $P < 0.001$) and significant interactions between direction and time ($F(2,14) = 44.51$, $P < 0.001$), and between direction and step size ($F(1,7) = 13.62$, $P = 0.008$). Post hoc tests showed a significant difference between T1 and T2 for both step sizes (small step: $t(7) = 4.83$, $P = 0.004$; large step: $t(7) = 6.53$, $P = 0.001$), but not between T1 and T3 (small step: $t(7) = 0.12$, $P = 0.911$; large step: $t(7) = 0.87$, $P = 0.606$). Hence, the vertical post-saccadic pursuit velocity increased according to our manipulation, but returned to normal after the end of the manipulation. This could mean that changes in post-saccadic pursuit velocity were rapidly re-adapted. To test for very short-lived
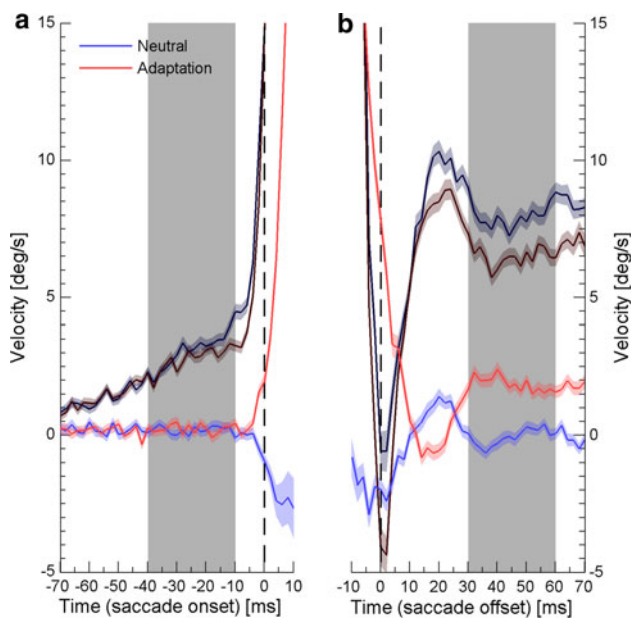
Fig. 7 Experiment 2: mean eye velocity traces in the last 100 adaptation trials (T2) across subjects. **a** Eye velocity before the first catch-up saccade, aligned to the onset of the saccade (*dashed line*). **b** Eye velocity after the first catch-up saccade, aligned to the offset of the saccade (*dashed line*). Traces are shown in *blue* for the neutral direction and in *red* for the adaptation direction; *dark colors* represent horizontal velocity; *bright colors* represent vertical velocity. *The shaded area* is bounded by the standard error of the mean. *The gray shaded areas* represent the time intervals over which we averaged pre- and post-saccadic pursuit velocity. Only data for the large step are shown

adaptation effects, we ran the same statistics after averaging data over a much shorter time-window, comprising the first 10 trials of the post-adaptation phase. Even in this case the difference between T1 and T3 failed to reach significance (small step: $t(7) = 0.98$, $P = 0.546$; large step: $t(7) = 2.45$, $P = 0.085$).

While the vertical velocity of pursuit was increased after the saccade, the horizontal velocity of pursuit was decreased by 16% in the small step condition [T1: 8.32 (SE 1.08); T2: 7.01 (SE 1.11); T3: 7.12 deg/s (SE 1.09)] and by 18% in the large step condition [T1: 8.01 (SE 0.93); T2: 6.54 (SE 1.00); T3: 6.94 deg/s (SE 1.01)]. The ANOVA showed a significant main effect of time ($F(1,7) = 27.61$, $P < 0.001$), indicating a non-directional modulation of velocity across phase. However, there was also a significant interaction between direction and time ($F(2,14) = 6.43$, $P = 0.010$), indicating a significant effect of the manipulation. Post hoc tests showed that the horizontal post-saccadic pursuit velocity differed significantly between T1 and T2 in the adaptation direction, with both step sizes (small step: $t(7) = 3.38$, $P = 0.023$; large step: $t(7) = 5.07$, $P = 0.003$) and between T1 and T3 (small step: $t(7) = 5.47$, $P = 0.002$; large step: $t(7) = 3.45$, $P = 0.021$). This shows

that while vertical pursuit velocity was increased after the saccade by our manipulation, the horizontal pursuit velocity was decreased. It indicates a change in the direction of pursuit, rather than an indiscriminate change in the gain of post-saccadic pursuit.

Finally, although we did not expect adaptation effects to be as strong for *pre*-saccadic pursuit velocity, which is generally much weaker than *post*-saccadic pursuit velocity in ramp paradigms, its analysis can provide an indication of the modification of visuo-motor gain by the manipulation (Fig. 7a). Adaptation increased slightly the vertical component of pre-saccadic pursuit velocity with the small step [T1: 0.04 (SE 0.16); T2: 0.18 (SE 0.14); T3: −0.12 deg/s (SE 0.19)] and with the large step [T1: −0.03 (SE 0.12); T2: 0.21 (SE 0.17); T3: 0.04 deg/s (SE 0.14)]. However, the ANOVA showed only a significant main effect of time ($F(2,14) = 9.13$, $P = 0.003$). Hence, adaptive changes of pursuit velocity were quite restricted to the post-saccadic period, and thus were unlikely to result from an overall modification of the visuo-motor gain of pursuit in the adaptation direction.

Discussion

We investigated the effects of position errors on saccade and pursuit adaptation. When we applied a target step either in or against the direction of target motion (Experiment 1), we obtained significant lengthening and shortening of saccade amplitude in the order of 11–15%, respectively, for both target speeds. Further, in that experiment, we found no clear indication of adaptation of the velocity of pre- or post-saccadic pursuit.

To confirm whether pursuit adaptation to position steps could be found, we performed a second experiment, in which we applied a target step in the vertical direction, orthogonally to the direction of target motion. For two different step sizes, we obtained a significant adaptation of the saccade vector. The magnitude of adaptation, in absolute value, scaled with the applied step size. Consistently with effects on saccades, we also observed a significant adaptation of the vertical component of post-saccadic pursuit velocity, in the sense of slow vertical eye movements, directed toward the displaced target, locked to the saccade offset. However, in contrast to saccade adaptation, pursuit velocity recovered rapidly to the pre-adaptation level in post-adaptation trials.

Catch-up saccades adaptation

We found reliable adaptation effects on catch-up saccades amplitude and trajectory, although the absolute size of the

errors we injected (on average ~ 0.7 and ~ 1.3 deg for the slow and fast target speed) and the amplitude of the saccades were much smaller than in most saccadic adaptation experiments (for a review Hopp and Fuchs 2004). Moreover, adaptation occurred over only some 200 trials, and presumably took place over the first trials (see Figs. 4, 6). Because with moving targets the required saccade amplitude is a function of the saccade latency and the presaccadic eye velocity, the resulting amplitude variability should make the adaptation longer compared to saccadic adaptation with a fixed target position at saccade onset (Straube and Deubel 1995). Our results thus show an astonishing ability of the saccadic system to keep a high sensitivity to systematic errors, even under the conditions of pursuit initiation.

Pursuit adaptation

At a basic level, smooth pursuit is conceived as controlled by a negative feedback loop that closes with a 100 ms delay (Lisberger et al. 1987; Keller and Heinen 1991; Newsome et al. 1985). Due to this delay, the first 100 ms of post-saccadic pursuit velocity rely on visual information gathered before the saccade onset. In adaptation paradigms in which pursuit is adapted to a velocity change locked to the first saccade onset, adaptation is driven by the velocity error (i.e., retinal slip) registered on the previous trials, similar to saccadic adaptation. Adaptation of pursuit initiation to a velocity change, as saccadic adaptation (Hopp and Fuchs 2004), can occur in the short-term and shows directional specificity (Kahlon and Lisberger 1996; Ogawa and Fujita 1997), with no generalization from one direction to the opposite direction.

Our saccadic adaptation paradigm was for the first time able to show adaptive changes of post-saccadic pursuit velocity driven uniquely by a position error. While target steps along the direction of target motion did not generate a strong adaptation, we found a clear adaptation in response to vertical steps. Those changes were not seen in pre-saccadic velocity, indicating that they do not result from an overall modification of the visuo-motor gain (Churchland and Lisberger 2002) in the adaptation direction.

Although a clear increase in pursuit velocity was found with vertical steps, we did not find a significant post-adaptation effect. If adaptive effects on smooth pursuit velocity truly resulted from neural plasticity, a readaptation effect should have been found. Variability in this measure was relatively high, and it could be that the readaptation to the previous adaptation state was too fast—and hence the effect size of the post-adaptation effects too small—to be noticed. More precise measurements would be required to settle this point.

Interaction between saccades and pursuit

Initially, saccadic and pursuit systems have been considered to be controlled by separate neural structures (Ilg 1997; Munoz 2002) and to respond to different signals (Rashbass 1961). In contrast, recent evidence suggests that there is a large overlap in the neural structures involved in smooth pursuit and saccade generation (for a review see Krauzlis 2004, 2005). Most notably, the superior colliculus (SC) may provide a motor error signal for both types of eye movements (Krauzlis et al. 1997, 2000; Krauzlis 2001, 2003).

The classical view postulated a clear-cut separation between the signals driving saccades and pursuit. Rashbass (1961), for instance, argued that position provides no input to the pursuit system because a target stepping in one direction and then moving in the opposite direction elicits a pursuit response in the direction of target motion and not in the direction of the step. However, Wyatt and Pola (1987) and Wyatt et al. (1989) reported an "oculomotor twitch", a transient pursuit eye movement in response to a step, with a peak velocity of some 0.7 deg/s and a latency of 100 ms, which can be triggered by passive or active fixation with steps larger than 0.25 deg. The authors suggested that apparent motion could be responsible for this effect, as indicated by the fact that the amplitude of the oculomotor twitch decreases when departing from the spatio-temporal range of apparent motion (Cavanagh and Mather 1989; Kolers 1972). It was also shown that in artificial open-loop conditions, in which the display is yoked to the eye position, target steps are able to generate a strong pursuit response (Pola and Wyatt 1980). It remains that under normal conditions, the influence of steps on pursuit was interpreted as due to the generation of a motion signal by a process of spatiotemporal interpolation (Carl and Gellman 1987), rather than as evidence for a strong influence of a position input, reflecting the difficulty of totally separating position and velocity inputs. Recently, however, a pure position signal (a flashed location) applied during maintained pursuit was shown to elicit a deviation of the direction of pursuit, perpendicularly to the direction of the pursuit target and scaled with eccentricity (Blohm et al. 2005). When a second stimulus appears in the periphery, perceiving apparent motion from the target to the new stimulus is unlikely. However, we may not rule out an attentional explanation, with the pursuit deflection reflecting an orienting response toward the flash, which is compatible with the finding that the inflection did not occur when the flash was task-irrelevant. Nonetheless, this adds to the early observation of Robinson (1965) that pursuit velocity can exceed the target velocity, to reduce small target offsets. As noted by Pola and Wyatt (1980), a sustained velocity overshoot makes a strong case for a position

input, as the retinal slip resulting from the increase in pursuit speed beyond target speed is in opposite direction to the retinal slip that should drive acceleration if velocity was the sole input. By showing that position can also drive adaptation of pursuit velocity locked to the end of the first saccade, we provide additional evidence for a position input to the pursuit system, as an accessory way of adjusting to dysmetric saccades.

On the other hand, even excluding apparent motion as an explanation, it might be that in the present study the intra-saccadic step is interpreted as an intra-saccadic speed change, which would be consistent with the effects we found on post-saccadic pursuit velocity. If a velocity change was inferred between the pre- and post-saccade period, rather than a position change, a step of 0.5 deg would then correspond to a speed change of 10 deg/s during 50 ms. Even integrating speed over a 100 ms period, we get a change in perceived velocity that could have caused the effects observed.

Whatever the signal driving pursuit adaptation is, adaptation of saccades and of pursuit is likely to be based on the adaptation of a unique internal model of the target trajectory. The comparison between the velocity and position of the target after the saccade with the predicted velocity and position provides the internal feedback that drives sensory-motor adaptation (Chen-Harris et al. 2008).

Previously, Nagao and Kitazawa (1998) studied adaptation to a change in target speed occurring during the first catch-up saccade and obtained adaptation of saccade amplitude and of the velocity of post-saccadic pursuit. One might argue that a position step was incidentally adapted in their manipulation, given that the speed change was likely to be perceptually suppressed during the saccade (e.g. Dodge 1900; Ross et al. 2001; Wurtz 2008), leading effectively to a mismatch in expected and actual target position after the saccade. In the context of saccadic adaptation, this point is supported by the absence of conscious detection of small displacements, more so when they are in the same direction as the saccade (Bridgeman et al. 1975; Wurtz 2008). We can calculate the potential position mismatch by multiplying the duration of the interval from the speed change to the saccade offset by the speed change (+10 or −5 deg/s). Nagao and Kitazawa applied the speed change when the catch-up saccade reached half the average amplitude. The duration of a catch-up saccade of 3.5 deg amplitude is of about 40 ms. We are left with a 20 ms period during which the changed speed might be perceptually suppressed. This would lead to a potential position error of 0.2 deg for the 10 deg/s velocity change and of −0.1 deg for the −5 deg/s velocity change. This represents at most 30% of the smallest position steps that we presented. A strong influence of the *perceived* step in Nagao et al.'s results is thus unlikely.

Neuronal correlates of adaptation

A crucial research question is at which processing stage adaptation takes place. One possible site is the superior colliculus (SC), which contains sensory and motor maps. These motor maps encode target locations for saccades (Wurtz and Albano 1980) as well as for pursuit (Hafed et al. 2008; Hafed and Krauzlis 2008; Krauzlis et al. 2000). Consequently, the SC has been related to saccade adaptation. However, the evidence is mixed. Albeit some neurons in the SC do not change their firing activity after saccade adaptation (Frens and Van Opstal 1997), they change their movement field (Takeichi et al. 2007), arguing for an adaptation upstream of the SC or in the SC. However, changes in movement fields may be independent from adaptation of the saccade vector itself, as shown recently by Quessy et al. (2010). Moreover, it is possible to adapt saccades that are elicited by electrical stimulation in the SC (Melis and van Gisbergen 1996), which suggests an adaptation downstream of the SC (see also Edelman and Goldberg 2002). This is supported by the finding that adaptation is transferred between express and targeting saccades, which rely differentially on the SC (Hopp and Fuchs 2002; Fuchs et al. 1996). Nonetheless, recent evidence suggests that the SC can still have a role in adaptation by providing an error signal, as shown by adaptation effects induced by microstimulation of the SC after the saccade offset (Kaku et al. 2009).

Several studies have identified the cerebellum as one of the structures involved in saccadic adaptation (Hopp and Fuchs 2004). In humans, it has been shown that patients with cerebellar lesions or cerebellar degeneration adapt less than normals (Golla et al. 2008; Straube et al. 2001). Differentiating between a fast and a slow adaptation process, it also has been shown that patients with cerebellar degeneration lack adaptation of the fast process, while the slow adaptation process is preserved (Xu-Wilson et al. 2009). An involvement of the cerebellum has also been shown with functional imaging (Desmurget et al. 1998). Studies with monkeys showed that an induced saccade dysmetry is not compensated if both the fastigial nuclei (FN) and the oculomotor vermis (OMV) are lesioned (Barash et al. 1999; Optican and Robinson 1980). A later study suggests that the origin of adaptation is upstream of the FN, probably in the OMV and that the FN relays the information. Although temporal inactivation of the FN disturbs adaptation during the inactivation period, residual adaptation can be observed after recovery of the FN in the dark (Robinson et al. 2002). This means that some hidden adaptation takes place, even when the FN is inactivated. At the single-neuron level it was shown that amplitude-reducing adaptation goes along with an increased firing rate of

neurons of a subregion of the FN feeding inhibitory burst neurons (Kojima et al. 2008).

For pursuit eye movements, sites in the cerebellum are also the most likely structures involved in adaptation (Thier and Ilg 2005). The OMV seems to play the same critical role as for saccade adaptation (Takagi et al. 1998, 2000). More specifically, the activity of Purkinje cells (P-cells) in the OMV correlates with saccade adaptation (Catz et al. 2008; Soetedjo and Fuchs 2006; Soetedjo et al. 2008), while the activity of P-cells in the floccular complex has been shown to be modulated by pursuit adaptation (Kahlon and Lisberger 2000).

Conclusion

By introducing a position error at the end of a saccade made toward a moving target, we showed that various compensation mechanisms are recruited in the short-term. Steps in the movement direction mainly elicited a decrease or increase in saccade amplitude. Steps in the orthogonal direction elicited an early or late inflexion of saccade trajectories and increased post-saccadic pursuit velocity in the direction of the step. Only recently studies have emphasized the need for an integrated saccadic and pursuit system (Erkelens 2006; Krauzlis 2004; Orban de Xivry and Lefevre 2007). We provide further evidence of interdependence by showing under some conditions synergic adaptation of the two systems to systematic position errors.

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