Short-term adaptation of saccades does not affect smooth pursuit eye movement initiation

Zongpeng Sun*

Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, Tübingen, Germany, Graduate School of Neural and Behavioral Sciences, International Max Planck Research School for Cognitive and Systems Neuroscience, University of Tübingen, Tübingen, Germany

Aleksandra Smilgin*

Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, Tübingen, Germany, Graduate School of Neural and Behavioral Sciences, International Max Planck Research School for Cognitive and Systems Neuroscience, University of Tübingen, Tübingen, Germany

Marc Junker

Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, Tübingen, Germany

Peter W. Dicke

Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, Tübingen, Germany

Peter Thier

Werner Reichardt Centre for Integrative Neuroscience, University of Tübingen, Tübingen, Germany

Scrutiny of the visual environment requires saccades that shift gaze to objects of interest. In case the object should be moving, smooth pursuit eye movements (SPEM) try to keep the image of the object within the confines of the fovea in order to ensure sufficient time for its analysis. Both saccades and SPEM can be adaptively changed by the experience of insufficiencies, compromising the precision of saccades or the minimization of object image slip in the case of SPEM. As both forms of adaptation rely on the cerebellar oculomotor vermis (OMV), most probably deploying a shared neuronal machinery, one might expect that the adaptation of one type of eye movement should affect the kinematics of the other. In order to test this expectation, we subjected two monkeys to a standard saccadic adaption paradigm with SPEM test trials at the end and, alternatively, the same two monkeys plus a third one to a random saccadic adaptation paradigm with interleaved trials of SPEM. In contrast to our expectation, we observed at best marginal transfer...
which, moreover, had little consistency across experiments and subjects. The lack of consistent transfer of saccadic adaptation decisively constrains models of the implementation of oculomotor learning in the OMV, suggesting an extensive separation of saccade- and SPEM-related synapses on P-cell dendritic trees.

Introduction

Human as well as nonhuman primates use saccades to shift their gaze to objects of interest and deploy smooth pursuit eye movements (SPEM) to keep the object image within the confines of the fovea, should it be moving not too fast relative to the beholder. Accurate saccades require the conversion of the retinal vector pinpointing the target into an appropriate motor vector. The relationship between the two is not fixed. Rather, matching the two requires the choice of appropriate parameters that will need updating in case the saccades generated may have failed to hit the target, for instance because the glasses worn by the beholder may change the metric of the retinal image. By the same token, the initial velocity of smooth pursuit in its early, still open-loop phase requires the choice and eventually updating of the parameters mapping target velocity onto eye velocity (Rashbass, 1961). Both forms of parametric adjustment are short-term as already the experience of only a few and at least in the case of saccades even only one exemplar of an inappropriate saccade or smooth pursuit eye movement may induce changes visible in following manifestations of the same oculomotor behavior (Collins, 2014; Havermann & Lappe, 2010; Srimal, Diedrichsen, Ryklin, & Curtis, 2008). And both saccadic learning (Barash et al., 1999; Golla et al., 2008; Optican & Robinson, 1980; Straube, Deubel, Ditterich, & Eggert, 2001) and SPEM learning (Dash & Thier, 2013; Ohki et al., 2009; Takagi, Zee, & Tamargo, 2000) depend on the integrity of lobules VI and VII of the vermis (the “oculomotor vermis” = OMV) as lesions of these lobules lead to severe—and most probably—irreversible loss of the ability to adjust the relevant parameters short term. The kinematics of saccades and smooth pursuit eye movements are grossly different. Whereas saccades are high velocity, short duration movements in which the eyes reach peak velocities of up to 1000°/s, smooth pursuit eye movements are confined to a range of small velocities not exceeding a few 10°/s (de Brouwer, Yule, Blomh, Missal, & Lefevre, 2002; Fuchs, 1967; Robinson, 1965; Westheimer, 1954), a range that is spared by even the slowest (= short amplitude) saccades (Martinez-Conde, Macknik, Troncoso, & Hubel, 2009). In view of the very different kinematic requirements of the two, one might expect that the cerebellar circuits for the control of saccade and SPEM kinematics are separate. Yet, contrary to this expectation, recordings from OMV output neurons, i.e., Purkinje cells (P-cells), in monkeys carrying out SPEM or saccades indicate that the OMV encodes the kinematics of both saccades and SPEM (Dash, Catz, Dicke, & Thier, 2012; Sun, Smilgin, Junker, Dicke, & Thier, 2017). As a matter of fact, rather than deploying distinct sets of P-cells, one tuned to the parameter space of saccades, a second one to that of SPEM, practically all OMV P-cells with oculomotor sensitivity are tuned to saccades as well as to SPEM (Sun et al., 2017). The OMV P-cell is the substrate of the short-term learning-based adjustment or adaptation of saccades (Catz, Dicke, & Thier, 2008) and of SPEM (Dash & Thier, 2013). Hence, one might expect that changes of a P-cell underlying short-term saccadic adaptation should affect SPEM, supported by the same P-cell. In other words, saccadic learning should spill over to SPEM. We tested this prediction in behavioral experiments on three monkeys in which we explored if short-term saccadic adaptation induced by two different regimes was transferred to catch trials of linear smooth pursuit. We observed at best marginal transfer, not very consistent over experiments and subjects. As both the adjustment of saccades and of SPEM depends on synaptic adjustments at the level of cerebellar P-cells, the low degree of transfer suggests an extensive separation of saccade- and SPEM-related synapses on P-cell dendritic trees.

Materials and methods

Animals and surgical procedures

Three rhesus monkeys (Macaca mulatta, males; M1–3; purchased from the German Primate Center, Göttingen, Germany) participated in this study, which tested for a transfer of short-term saccadic adaptation to SPEM initiation. The experiments on these animals including the surgical and behavioral protocols were approved by the local animal care committee, conducted in accordance with the guidelines of the National Institutes of Health for Care and Use of Laboratory Animals and supervised by the veterinary authorities (Regierungspräsidium Baden-Württemberg und Landratsamt Tübingen). M1 and M2 participated in an experiment in which saccadic adaptation was induced by exposing the monkey observers to the same visual error over a longer series of trials (“consistent error” adaptation experiment). In a second experiment, which involved M1, M2 and M3, we deployed a random error paradigm in which adaptation of saccades in trial n was induced by presenting a visual error in the preceding trial n-1, whose direction flipped randomly. All monkeys underwent a surgical proce-
dure needed to implant a titanium head post and scleral search coils. The head post was required to painlessly restrict the head movements during experiments. The search coil allowed the high-resolution measurement of instantaneous eye position by picking up a small, eye position-dependent voltage induced by an alternating magnetic field around the monkey’s head (Fuchs & Robinson, 1966; Robinson, 1963). The surgical procedures used were identical with those in previous studies (Sun et al., 2017) and described in more detail there. Briefly, monkeys were anesthetized using a combination of isoflurane and remifentanil while carefully monitoring all vital parameters [body temperature, carbon dioxide, oxygen, blood pressure, electrocardiography (ECG)]. Animals were supplied with analgesics until any signs of pain disappeared and allowed to fully recover before conducting the experiments. Each monkey was trained to voluntarily come to his customized primate chair. During experiments they were seated in the chair at a distance of 40 cm in front of the CRT monitor in complete darkness. Each monkey was extensively trained to execute precise saccades and SPEM. The motivation to participate in the experiments was achieved by asking the monkeys to cover their daily fluid intake needs by complying with the behavioral demands. Specifically, each successful eye movement trial was rewarded with water. If needed, additional fluid and/or juicy fruits were provided after experiments to satisfy the daily fluid requirements. However, the monkeys did not get water in their home cages during periods of work. Usually every fortnight, they were granted a two-day vacation with free access to water and juicy fruits in their home cages. Each animal was regularly inspected by the university’s veterinarians to ensure that they were in good health.

Behavioral tasks

The visual stimuli were presented on a 22-in diameter Cathode Ray Tube monitor (Ilyama MA203DT) operating at 88 Hz and at a resolution of 1600 × 1200 pixels. For the control of the experiments as well as data acquisition, we deployed software developed in house freely available (nrec, http://nrec.neurologie.uni-tuebingen.de), running under Linux on a standard PC.

Eye position calibration

The eye movement signal delivered by the scleral search coil was sampled at 1 kHz. Prior to each experimental session it was calibrated using the known position of a white fixation target (dots diameter: 0.4°) that appeared at random on the monitor in one out of nine positions defining a 30° × 30° grid centered on straight ahead. Monkeys were asked to maintain fixation at each target for approximately 1 s in order to get a liquid reward and then to proceed to the next cued location. The data acquired was subjected to a regression analysis that considered linear, quadratic and mixed term dependencies in order to predict eye position based on the search coil voltage.

Visually guided saccades and saccadic adaptation

A visually guided saccade trial consisted of a fixation period of 500–1000 ms, after which the fixation target (white dot, diameter: 0.4°) was replaced by a target of the same appearance presented at 10° horizontal eccentricity, eliciting a visually guided saccade (Figure 1A, top row). The monkey was rewarded if he was able to keep his eyes within the confines of an invisible squared fixation window of 1.5°–3° side length. In order to prompt saccadic adaptation, the peripheral target originally presented at an eccentricity of 10° jumped to a new position (an eccentricity of 7° or 13° depending on the direction of adaptation) during the execution of the visually guided saccade. In order to trigger the target jump, we used an analogue saccade detector that determined the point in time at which the eye velocity signal crossed a preset velocity threshold, triggering a target shift of either 3° outwards (saccade outward adaptation experiments) or 3° inwards (saccade inward adaptation experiments). These intrasaccadic target shifts induced a secondary corrective saccade bringing the eyes closer to the final target location (Figure 1A, middle row).

Smooth pursuit eye movements

In SPEM trials, a white 0.4° target was presented in the center of the screen for 500–1000 ms, and the monkey was required to maintain fixation. Then this central fixation target jumped to a new location 1.4°–2.4° (chosen depending on the properties of a subject’s initial SPEM, see below) from the original straight ahead position on the horizontal and started to move in the opposite direction with a constant velocity of 12°/s (Figure 1A, bottom row). The purpose of the initial target step was to ensure that the subsequent target ramp would have moved the target back to straight ahead at the time of SPEM onset, thus reducing the need to generate an early catch-up saccade (Rashbass, 1961).
Transfer of saccadic adaptation with consistent target shifts to SPEM

The experimental session started with 40 baseline SPEM trials as described before and ended with 40 test SPEM trials. The initial block of SPEM trials was followed by a block of trials in which the monkey was asked to carry out saccades towards an eccentric target, followed by a block of 500–1000 saccadic adaptation trials in which the target was shifted either consistently outward or inward by 3°, thereby inducing outward or inward saccadic adaptation (McLaughlin, 1967; Figure 1B and C). The direction of the SPEM and saccades was consistent for a particular session either to the left or to the right.

Transfer of random saccadic adaptation to SPEM

Visually guided saccades, saccadic outward and inward adaptation trials, and SPEM were presented in random order in blocks of about 200 trials. In individual sessions the direction of SPEM and of primary saccades was consistent either to the left or to the right. In saccadic adaptation trials, the target jumped from its initial location at 10° during the

Figure 1. Experimental paradigms. (A) Exemplary saccade trial, followed by a saccadic adaptation trial prompting gain decrease adaptation and a SPEM trial. (B) Sequence of events in the consistent error experiment with errors causing saccadic inward adaptation. (C) Sequence of events in the consistent saccadic error experiment causing outward adaptation. (D) Sequence of events in the experiment on the transfer of random saccadic errors to SPEM. Five exemplary consecutive trials are shown. Note that the amplitude of the primary saccade in the second trial increased due to the preceding outward adapting saccade trial. (E, F) Detection of saccades (left) and SPEM (right). The top panels show plots of eye position as function of time (bottom) for exemplary saccade and SPEM trials; the lower panels, eye velocity. The vertical dashed lines indicate eye movement onset determined as described in Methods. The horizontal dashed lines in the velocity plots give the velocity thresholds used and the red lines in the SPEM velocity plot represent the two intersection regression lines pinpointing SPEM onset. The shaded area indicates the period of open-loop SPEM.
primary saccade to a new one at 7°, 8°, 9°, 11°, 12° or 13°, each possible location chosen at random with equal probabilities. The probability of SPEM and saccade trials was 50% each (Figure 1D).

**Data analysis**

Data processing and statistical analysis was based on custom written routines in MATLAB (The MathWorks Inc., Natick, MA).

The onset and offset of a saccade were detected using an eye velocity threshold of 20°/s (see Figure 1E). In the saccadic adaptation experiment with consistent error, the gain was calculated by dividing the mean saccade amplitude of the last 40 saccade trials by the mean amplitude of the first 40 saccade trials of the session. The saccadic adaptation gain in the random saccadic adaptation experiment was calculated for each session by dividing the mean saccade amplitude for a particular class of target shifts (i.e., from 10 to 11, from 10 to 9, etc.) by the mean saccade amplitude of all trials without target shifts that preceded them.

The saccadic visual error (SVE) in the random saccadic adaptation experiment was defined as the difference between the final target location and the saccadic end position of the first saccade after the first target shift.

Each SPEM trial was visually inspected. The detection of the onset of SPEM required several steps. First, we determined the point in time at which the velocity exceeded the mean eye velocity in the first 80 ms after the target backshift by three standard deviations for 40 consecutive milliseconds. Then two regression lines were computed: one on the eye velocity during the 200 ms before this time point and a second one on the following 15 ms (as shown in Figure 1F). The interception of these two regression lines was then taken as the time of SPEM onset. Trials including saccades in the first 200 ms of the SPEM as well as trials in which the careful visual inspection suggested that the automatic onset detection had obviously failed to identify SPEM onset were excluded. In the saccadic adaptation experiment with consistent error, SPEM gain was taken as the ratio of the mean peak velocity in a period of 0–150 ms (open-loop SPEM, highlighted in Figure 1F) after SPEM onset of the last 40 SPEM trials divided by the mean peak velocity of the first 40 SPEM trials. The SPEM gain in the random saccadic adaptation experiment was calculated in the following way: The peak velocity of SPEM in trials following saccadic adaptation trials with target shifts from one of the six classes was divided by the mean peak velocity of all SPEM trials, which were preceded by saccade trials without target shift.

**Effects of consistent visual errors on saccades**

We collected a total of 40 experimental sessions (20 with inward errors, 20 with outward errors, 10 from each subject). Each session started with 40 baseline SPEM trials, followed by 40 visually guided saccades and then either by consistent saccadic outward or inward trials. The session then ended with 40 test SPEM trials. Figure 2 depicts exemplary sessions, one with an outward error (Figure 2A) and one with an inward error (Figure 2B), documenting the expected amplitude increase and decrease respectively with trial number. Over all sessions, saccadic gain increased on average by 14% in the case of outward adaptation and decreased by 19% in the case of inward adaptation (Figure 2D). As documented by the exemplary velocity traces in Figure 2C and the group data in Figure 2E and F the gain changes were the result of a decline in peak velocity not compensated by changes in saccade duration in the case of inward adaptation (\(p = 0.0004,\) Wilcoxon signed rank test) and by an increase of saccade duration associated with constant saccade peak velocity in the case of outward adaptation (\(p < 0.01\)). The differential effects of inward and outward adaptation on saccade velocity and duration are in accordance with previous findings (Prsa, Dicke, & Thier, 2010).

We next asked whether the changes of saccade metrics due to inward or outward shifts of the target had any effect on the following SPEM tested in a block of trials (SPEM test block) following the adaptation block. To this end, we compared the mean peak velocity of SPEM in the block of trials before a saccadic adaptation block (SPEM baseline block) with the peak velocity of SPEM test trials (Figure 3). The comparison was based on a consideration of the first SPEM test trial, probably the one most affected by the preceding saccadic adaptation trials and a consideration of the mean performance in the test block, arguably better able to reveal subtle changes persisting longer than a few trials. The peak velocity of the first SPEM trial after a saccadic adaptation block did not change significantly, neither in the case of outward nor in the case of inward adaptation (Wilcoxon signed rank test outward: M1: \(p = 0.32,\) median = 0.92; M2: \(p = 0.38,\) median = 1.02, inward: M1: \(p = 0.7,\) median = 1.04; M2: \(p = 0.92,\) median = 1.02). In the case of saccadic outward adaptation the comparison of the mean peak velocity of all SPEM trials in one subject (M1) failed to reveal any transfer. The other subject (M2) exhibited a tiny, yet significant decrease in its mean SPEM peak velocity, i.e., a change that is opposite to a true learning transfer effect (M1: \(p = 0.11,\)
median \( \approx 1.03; \) M2: \( p = 0.04, \) median \( \approx 0.97, \) Wilcoxon signed rank test). In the case of saccadic inward adaptation, both subjects showed significant changes. Whereas subject M2 exhibited a decrease, consistent with a transfer of learning transfer, M1 showed an increase in average peak velocity SPEM, i.e., a change that is opposite to a transfer effect (M1: \( p = 0.02, \) median \( \approx 1.04; \) M2: \( p = 0.004, \) median \( \approx 0.94, \) Wilcoxon signed rank test; Figure 3A). Hence, overall significant changes obtained were few and inconsistent and hardly supporting the notion that substantial saccadic learning would transfer to SPEM. We wondered if the significant changes observed might not actually have been artifacts of longer term behavioral trends. For instance a general decline in performance over time, due to cognitive fatigue might feign as transfer of gain-decrease adaptation. If performance had indeed changed continuously over time, one might expect to see changes in SPEM velocity also along the sequence of the 40 SPEM test trials. However, no significant differences in SPEM velocity were obtained when we compared the first half of SPEM test trials after saccadic adaptation with the second half in any of the monkeys, neither for inward nor for outward adaptation experiments (\( p > 0.05, \) Wilcoxon signed rank test). While this negative result does not support an influence of longer term performance changes, it does not necessarily rule it out as changes within a block of only 2 \( \times \) 20 trials may have been too subtle to stand out. Independent of the question as to the relevance of long-term behavioral trends, the suspicion that the small and somewhat inconsistent changes observed at the transition from saccadic adaptation to the SPEM test block may not necessarily reflect true learning transfer is also nourished by the fact that a direct comparison of test block SPEM velocity between outward and inward experiments revealed few differences. We considered both the first test block trials and the averages across the test blocks. The only significant difference was obtained for M2 who exhibited larger peak eye velocities in the test block after gain increase adaptation when considering the average across the test block trials (\( p = 0.014, \) Wilcoxon signed rank test).

We also analyzed the influence of saccadic adaptation on the peak acceleration in the first 150 ms of SPEM. Similar to our approach to peak velocity, we compared this kinematic measure in the first trial of SPEM after saccadic adaptation and its mean over all test block trials with mean peak SPEM acceleration in the baseline block. As summarized in Figure 3B (first SPEM trial: outward: M1: \( p = 0.92, \) median \( = 0.97; \) M2: \( p = 0.19, \) median \( = 0.85; \) inward: M1: \( p = 0.19, \) median \( = 0.82; \) M2: \( p = 0.38, \) median \( = 1.11; \) all SPEM trials: outward: M1: \( p = 0.43, \) median \( = 0.95; \) M2: \( p = 0.04, \) median \( = 0.89; \) inward, M1: \( p = 0.32, \) median \( = 1.04; \) M2: \( p = 0.13, \) median \( = 0.95), \) neither saccadic gain
As individual sessions differed regarding the number of saccadic adaption trials, we checked if the number of saccadic adaptation trials mattered for SPEM gain based on the average of all test block trials. As shown in Figure 3D, the plot of SPEM gain as a function of the number of saccadic trials did not reveal a significant relationship between the two (first SPEM trial: $p = 0.2$, $r = 0.21$; all SPEM trials: $p = 0.18$, $r = -0.22$).

Effects of random visual error on ensuing saccade

Just one or a few SPEM trials might suffice to largely reset the saccadic adaptation achieved. In this case measures of SPEM based on the mean performance in the first trial of the test blocks would hardly be able to reveal any transfer. The reason is that the number of experimental sessions and therefore the number of first trials is comparatively small which is why subtle remaining transfer effects may simply be hidden by noise. This consideration was the reason to embark on a second series of experiments, resorting to a random error design, allowing us to substantially increase the number of potential transfer trials. The approach chosen was guided by previous demonstrations of clear saccadic adaptation prompted by a visual error in the immediately preceding saccade trial (Collins, 2014; Havermann & Lappe, 2010; Srimal et al., 2008). In order to verify the trial-by-trial effects of saccadic adaptation on the open-loop SPEM initiation, we collected a total of 25,573 trials from three subjects.

In order to assess the effect of a visual error in a saccade trial on the saccadic amplitude in a subsequent saccade trial, we separated the saccade trials according to the target shift in the preceding trial into three groups: an adaptive outward target shift independent of its size, an adaptive inward target shift independent of its size, and saccade trials preceded by SPEM. Saccades made in trials following trials without preceding target shifts were hypometric in all three subjects. The median visual errors of all sessions were $-1.39^\circ$, $-0.83^\circ$, and $-1.07^\circ$ for M1, M2, and M3 respectively. In each session these saccades served as reference for the others, setting their amplitudes to 1 (Figure 4A). All three subjects showed normalized saccade amplitudes significantly smaller than 1 for saccade trials preceded by trials with inward shifts of the saccade target ($p < 0.01$, Mann-Whitney $U$ test). Accordingly, the normalized amplitude of saccades with preceding outward shifts of the saccade target was significantly larger than 1 ($p < 0.01$, Mann-Whitney $U$ test). Unexpectedly, the saccade trials preceded by SPEM trials also exhibited a tiny, yet significant gain increase ($p < 0.01$, Mann-Whitney $U$ test).

As shown by Figure 4B, which plots normalized saccade amplitude as a function of the size and
direction of the target shift in the preceding trial, the modification of saccade amplitudes clearly scaled with target shift size in the preceding trial ($r = 0.9689$, $p = 0.0014$, slope = 0.026). As a consequence of the variability of saccadic responses, the saccadic visual errors (SVEs) associated with trials in which the target exhibited a particular shift behavior also varied. It is the actual size of the SVE in a given saccade trial that determines the size and direction of adaptation in the ensuing saccade trial, which is indicated by the significant correlation between SVE in trial n-1 and saccade gain in trial n ($r = 0.978$, slope = 0.005; Figure 4H) and SVE (Figure 4I) respectively in trials n-1 and saccade duration in trials n.

Effects of random saccade errors on ensuing SPEM

To evaluate the trial-by-trial effects of saccade errors and saccadic adaptation on the gain of the open-loop SPEM response in interleaved trials of SPEM, we grouped SPEM trials based on the features of the one back and two back saccade trials. We distinguished four cases: A given SPEM trial could have been preceded by either one saccadic inward or outward adaptation trial (trial n-1), or preceded by two sequential inward or two sequential outward adaptation trials (n-1 and n-2). Figure 5A compares the mean open-loop SPEM peak velocity for these four groups, separately for the three monkeys.
Whereas monkeys M1 and M3 did not exhibit a significant effect of preceding saccadic adaptation trials on the velocity of the open-loop SPEM for any of the four cases distinguished \( (p > 0.01, \text{Mann-Whitney } U \text{ test}) \), monkey M2 showed a small (3\%) yet significant decrease of his open-loop SPEM peak velocity if the SPEM trial was preceded by two inward adaptation trials \( (p = 0.0003, \text{Mann-Whitney } U \text{ test}) \).

In order to capture potential changes in open-loop SPEM peak velocity due to the size of the SVE in the immediately preceding saccade trial, we plotted SPEM velocity as a function of preceding SVE for each individual subject (Figure 5B). We obtained significant linear regressions for two of the three monkeys (M1, M2). Yet, the slopes of the resulting linear regressions were without exception very close to 0, indicating that the effect of SVE on SPEM peak was in any case subliminal.

**Discussion**

In this study we addressed the question if saccadic adaptation prompted by a history of prior saccadic errors transfers to the open-loop segment of ensuing SPEM. Saccadic adaptation was either induced by a sequence of consistent target shifts during saccades or, alternatively, by target shifts whose size and direction was chosen randomly from six classes. Both paradigms elicited clear saccadic adaptation with features in accordance with previous work (Noto & Robinson, 2001; Robinson, Noto, & Bevans, 2003; Srimal et al., 2008; Wallman & Fuchs, 1998), such as the velocity decrease but no change of duration caused by inward adaptation, and prolongation of duration but no change of velocity in the case of outward adaptation. Yet, independent of the paradigm chosen, significant influences on test SPEM following saccadic adaptation were absent in most of the cases, if present often in a direction opposite to the direction of learning transfer and in any case tiny, reflecting only a very small fraction of the adaptation-based changes of saccades. Most of the few cases of minimal change were obtained when running the consistent target shift paradigm. As any consistency in trial structure has the potential to cause long-term behavioral changes, e.g., due to cognitive fatigue and thereby changes in performance over time, we were concerned that the transition effects might have been confounded by such trends. While our control analysis could not support this concern, more subtle changes of performance over time in the first experiment, building on consistent shifts of the saccade target, cannot be excluded. One of the virtues of the second experiment, characterized by a completely randomized trial structure, was that it was optimally suited to prevent the confounding influence of time-dependent performance changes on potential learning transfer. Using this paradigm, we observed a significant decrease in open-loop SPEM peak velocity in one (M2) of the three monkeys in individual SPEM trials following saccadic adaptation trials if the SPEM trial was preceded by two trials of saccades with target shifts in an inward direction. Yet, this transfer effect was tiny, amounting to a drop in peak velocity of 3\% only. This percentage must be compared to the 6\% decrease of the amplitude of saccades, preceded by only one trial of saccades with inward shift in the random saccadic adaptation experiment. That transfer effects—if detected at all—are indeed very small, is also supported by the minimal slopes of regressions of the size of the visual error in saccade trials preceding SPEM trials in the random saccadic adaptation paradigm.

Our finding that short-term saccadic adaptation has small, albeit quite inconsistent, effects on the kinematics of the ensuing SPEM may support a role of small savings from learning. However, even if such small savings from saccadic learning existed, the need to perform SPEM as precisely as possible might easily
overcome the savings, thereby concealing their influence. Crosstalk between saccades and SPEM is not confined to saccadic learning. Also catch-up saccades may affect the velocity of postsaccadic pursuit (Schutz & Souto, 2011). Actually, in this case the impact seems to be much stronger and more consistent than the small and somewhat inconsistent learning transfer seen in our experiments. This difference may be a consequence of the distinct requirements of catch-up saccades which have to take the velocity of the moving target into account, a condition which is different from normal visually guided saccades (de Brouwer, Missal, & Lefevre, 2001).

Our study demonstrates some evidence for transfer of learning in short-term adaptation tasks, a form of adaptation that is based on adjustments at the level of individual Purkinje cells (Catz et al., 2008). Although minimal and not very consistent over experiments and subjects, and therefore probably not too relevant in functional terms, the demonstration of occasional transfer is in line with the notion that the same OMV P-cells convey saccade and SPEM information. It is commonly held that saccadic learning and other forms of cerebellum-dependent learning are based on changes of the strength of parallel fiber synapses (Albus, 1971; Marr, 1969). If OMV P-cells deployed largely congruent sets of parallel fiber synapses for the control of saccades and SPEM, we might have expected stronger and more consistent transfer effects. In other words, the minor crosstalk observed argues for synaptic territories for saccade- and SPEM-related parallel fiber input on P-cell dendritic trees that are largely separate. However, reserving distinct pools of synapses for saccades and for SPEM would only help if also the mossy fiber (MF)-PF signals for saccades and SPEM offered to OMV P-cells formed functionally distinct and anatomically segregated pools. The finding of unrelated preferred directions of P-cell simple spikes for saccades and SPEM would be compatible with this assumption (Sun et al., 2017). However, it is questionable if and to what extent the requirement of segregation is really met. Although for instance MF-PF input from the paramedian reticular formation (PPRF; Gerrits & Voogd, 1986; Thielert & Thier, 1993) devoted to saccades (Hepp & Henn, 1983) complies with this requirement, a substantial fraction of eye movement-related neurons in the dorsal pontine nuclei (DPN), another source of MF-PF input to the OMV, are responding to saccades as well as to SPEM (Dicke, Barash, Ilg, & Thier, 2004). The latter might actually suggest that the duality of OMV P-cells is an inevitable consequence of the tight integration of information on saccades and SPEM on the input side as witnessed by the DPN but also other structures such as the reticular nucleus of the pontine tegmentum (NRTP; Giolli et al., 2001) and superior colliculus (Krauzlis, 2003). We cannot say if the overlap between saccade and SPEM input to OMV P-cells is strong enough to override the impact of afferent fibers specifically devoted to the one or the other type of eye movement. In the case of dominating dual eye movement input, probably the only way to explain the observed small and inconsistent transfer would be to assume that the sensitivity of the behavioral tasks deployed may have been too poor to unravel larger savings of learning. Although this reservation has to be made, we think our demonstration of little transfer of saccadic adaptation SPEM, undoubtedly involving cerebellar P-cells, rather argues for distinct synaptic pools on P-cell dendritic trees, one reserved for saccades, the other one for SPEM.

**Keywords:** saccadic adaptation, smooth pursuit eye movement, Purkinje cell, cerebellum, rhesus monkey

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* ZS and AS contributed equally to this work. Commercial relationships: none. Corresponding author: Peter Thier. Email: thier@uni-tuebingen.de. Address: Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, Tübingen, Germany.

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