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RESEARCH ARTICLE

Sustained effects for training of smooth pursuit plasticity

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Abstract Maintaining orientation in space is a multisensory process, with the vestibular, visual, auditory and somatosensory systems as inputs. Since the input from each individual system changes, for example due to aging, the central nervous system must continuously adapt to these changes to maintain proper system performance. Changes can also be elicited by targeted modifications of the inputs, or by controlled training of sensory systems. While the effects of adaptation on eye movements elicited by the vestibulo-ocular reflex are well established, modifications of the efficacy of smooth pursuit eye movements are less well understood. We have investigated whether two 6-min training sessions on three subsequent days can induce lasting changes in the open- and closed-loop smooth pursuit performance of healthy, adult subjects. Ten subjects practiced making pursuit eye movements by tracking a target cross which moved quasi-randomly on a computer screen. Smooth pursuit performance was tested with a step-ramp paradigm immediately before and after the training, as well as 5 days after the last training session. Our results show that even such short training sessions can induce significant, lasting improvements in closed-loop smooth pursuit performance if the pursuit system of the subjects is challenged sufficiently during training. Control experiments on ten additional adult subjects who had their pursuit performance tested before and after a 20 min break without visual training confirmed that the pursuit enhancement is due to the visual training and not due to perceptual learning.

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Introduction

We obtain information about our environment and our orientation in it from multisensory inputs. The different sensory and sensory-motor systems strongly interact with each other. Since the contribution from each individual system changes over time, either due to natural aging processes or due to accidents or diseases, the central nervous system has to continuously adapt to these changes. The present study investigates changes in our eye movement patterns that can be elicited by sensorimotor visual input.

Eye movements can be separated into two distinct types: slow, smooth pursuit eye movements, which enable us to accurately track slowly moving targets by stabilizing the target image on the retina, and fast, saccadic eye movements, which shift and realign the direction of gaze. When the head is moving, the vestibular and visual systems are strongly coupled to ensure clear vision during locomotion (Leigh and Zee 1999).

The performance of the visual system has been investigated by modifying different sensorimotor parameters. For example, we know how changes in the visual input—which can be elicited by wearing magnifying glasses or prisms—can modify eye movements when the head is stationary (Redding et al. 2005; Rode et al. 2006). We also know that changes in the visual input can modify reflexive eye movements as elicited by the vestibulo-ocular reflex (VOR), where a number of studies showed that both slow and fast responses of the visual system can be targeted (Pelisson et al. 2010; Schubert and Zee 2010; Shelhamer et al. 2005).

Eye movements also change with the mechanics of the oculomotor plant. Kommerell et al. (1976) were among the first to report plasticity of the saccadic system in patients with partial abducens nerve palsies. The same applies to the pursuit system. Optican et al. (1985) showed that not only the saccadic but also the smooth pursuit system adapts in response to monocular muscle weakness. During that experiment the patients were forced to view their scenery with the impaired eye while the healthy eye was occluded. Movements of the impaired eye improved significantly after a short adaptation period of a few days. While the complete adaptation took several days, the reversal to the initial state was much quicker. More recently, Thier and Ilg (2005) showed that the delay in the initiation of pursuit can be reduced by the experience of later changes in the speed of the target presented.

Less is known about modifications of eye movements due to changes in the vestibular system, or changes that are related to systematic visual training. However, investigations have shown that such modifications do occur. Bockisch et al. (2004) investigated the smooth pursuit eye movements of a group of patients with bilateral vestibular loss. Their results indicated that within this group of patients, only people with improved smooth pursuit response adapted well to the vestibular dysfunction in daily life. Loader et al. used the connection between the visual system and balance to increase postural stability in patients with vestibular asymmetry and resulting disequilibrium. Twenty-four subjects with chronic disequilibrium were divided in a treatment group and a control group without visual training (Loader et al. 2007). Those patients undergoing the rehabilitation procedure showed significantly higher performance when tested with a “Sensory Organization Test”, a protocol which identifies abnormalities in the patient’s use of somatosensory, visual and vestibular inputs. Their results indicated that simple visual training could be an effective rehabilitation method to treat patients with vestibular disorders. This is consistent with recent findings by von Lassberg et al. (2012), who showed that regular gymnastics training significantly increases smooth pursuit performance.

Even visual activities alone can modify the execution of eye movements. Fukushima et al. 1996) showed that short-term adaptation of the late component of the initial eye velocity can also be induced by visual training. They investigated six subjects and evaluated their ability to follow a step-ramp paradigm immediately before and after a 30-min training session. But it remains unknown to what extent such improvements of the smooth pursuit performance can be accrued, and how long they can last when the training has stopped. We believe that this point is important, especially considering that a substantial fraction of patients presenting with dizziness cannot be diagnosed with either peripheral or central disorders, and many well understood vestibular deficits cannot be treated surgically or with medication. For this large group of patients it is important that their existing sensorimotor resources are optimally used to compensate for their vestibular deficits and for their idiopathic dizziness problems. The motivation of our study is to investigate whether simple visual training can lead to significant and lasting effects on smooth pursuit eye movements, which could then compensate for deficits in the vestibular response. An application for this could be the development of video based training paradigms for visual rehabilitation, which could be performed either at a rehabilitation center or at residential homes for elderly, or as a self-guided home therapy as part of daily training for treatment of dizziness and vertigo of unknown origin.

Methods

Subjects

All subjects were volunteers and had a visual acuity between ±1 diopters and astigmatism of less than 1 diopter for any axis. This allowed us to perform pursuit experiments without subjects wearing contact lenses or glasses during the recordings. Upon questioning, none of the subjects reported any previous or current vestibular or oculomotor problems, or taking any medication likely to affect eye movements. Since it has been shown that “heavy computer gaming” (i.e. playing computer games for many hours every day) can affect the performance of eye movements (Ilg and Mack 2010), we ensured that none of our subjects fell into the category of “heavy gamers”. None of the subjects had previously participated in visual or vestibular training studies.

We divided our subjects into two groups: a training group of subjects who performed the eye movement training as described below; and a control group, who underwent the same testing procedures but performed no additional eye movement training. The training group consisted of ten volunteers (two female, eight male) with an average age of 26 ± 1.9 years (mean ±1 standard deviation; range 24–30 years); the control group consisted of ten further volunteers (six female, four male), aged 23 ± 0.7 years (range 22–24). While age and gender of the two groups do not match exactly, no age related decline in sensory function has been reported for subjects under 40 years. Poole (1992) reported a decline of sensory systems after the age of 40, and Knox et al. (2005) documented an age related increase of pursuit latency whilst comparing older subjects (72 ± 6 years) with younger ones (21 ± 2 years). However, there is no indication of age-related changes of eye movements in the age group spanned by our participants.

The experiments were approved by a local ethics committee, and were in accordance with the 1964 Declaration of Helsinki. All subjects gave their informed consent to participate prior to their inclusion in the study.

Apparatus

Horizontal and vertical eye positions were recorded using an EyeSeeCam (University of Munich Hospital, Clinical Neurosciences, EyeSeeCam, Munich, Germany) video-oculography (VOG) system (Schneider et al. 2009). Eye positions were sampled at 220 Hz, as preliminary experiments had indicated that sampling rates above 100 Hz facilitate the data analysis, for example the calculation of gain as described below. In order to record with this sampling rate, the video field of view was reduced to an area of 348 × 216 pixel, which was sufficient to track the movement of the pupil. Head and body movements of the subjects were restricted by using a chinrest and a compressive vacuum cushion for the head. For both the eye movement recordings and the visual training the subjects were seated in a dark room (2 × 2.2 × 1.2 m: length × height × width), 54 cm in front of a 21″ cathode ray tube (CRT) monitor (Dell UltraScan 21TE, maximum luminance ca. 300 cd/m^2). This setup enabled a viewing angle of 45° in the horizontal plane and 35° in the vertical plane. The monitor was operated at 75 Hz with a resolution of 1,280 × 800 pixels via a Mac Book (Model A1181) outside the dark room. The Mac Book was used to generate the visual training paradigm, for operating the EyeSeeCam system, and for generating the evaluation and calibration paradigms. After the experiment, the data were analyzed offline in Matlab (MathWorks, Matlab, Natick, MA, United States). For the generation of the visual stimulus, the open source Matlab based "Psychtoolbox" (Brainard 1997; Pelli 1997) was used.

Eye position was represented as pixel values extracted from the VOG system. The position in degrees was calculated using the data gained by the calibration procedure. For this calibration the subjects had to look at a white dot on a black screen directly in front of them and 8.5° to the left, right, up and down.

Paradigm

For training and testing, the visual target was a white cross with a diameter of 1.5° and a black dot with a diameter of 0.2° in the center. To enhance smooth pursuit performance the target was presented on a black background for maximum visual contrast (Barnes 2008). The subjects were told to focus on the black dot in the middle of the white cross. Two different visual stimuli were used for the study: one quasi-random stimulus for the visual training of the subjects, and a step-ramp stimulus for the evaluation of open and closed loop gains of the smooth pursuit eye movements before and after the training sessions.

During training, the target moved across the screen in a quasi-random style (Fig. 1a).

To guarantee a non-predictable, challenging movement, the target movement was designed as a superposition of 120 sine waves with randomized frequencies ranging from 0.05 up to 0.4 Hz in the horizontal and vertical plane. Amplitudes were randomized between 0 and 1, and phase shifts between 0 and 2 * pi. After summation, a weighting function in the form of a hyperbolic tangent was applied to the amplitude such that the resulting movement covered the whole screen. For our training stimulus and for subjects sitting 54 cm in front of the CRT, the resulting maximum horizontal velocity was 41.1°/s (mean ±1 standard deviation of the absolute velocity: 11.9 ± 6.8°/s) and maximum vertical velocity was 35.5°/s (10.3 ± 5.8°/s). The training paradigm was saved as video file (AVI-format, Cinepak-codec). This makes visual training independent of a Matlab environment and of any operating system, increasing the feasibility of possible home use. The video was displayed at 75 Hz (which matched the monitor refresh rate) and shown via the VLC media player (VideoLAN Organization, VLC Media Player, Paris, France).

For the evaluation paradigm, we chose a step-ramp trajectory as suggested by Rashbass (1961) in order to suppress the initial saccade, since in the presence of an initial saccade the open loop pursuit performance is hard to analyze. The step was chosen such that the target crossed back over the origin after 150 ms (Rashbass 1961), as shown in Fig. 1b. To investigate the effect of different target velocities, three different velocity steps were used, from 0 to 10, 20 and 40°/s, respectively. Target speed, direction (right or left) and starting position were randomized. Between every two trials, the subject was sitting in the dark for a random period between 2 and 5 s. To ensure that each trial led to a valid measurement only a limited area of the screen was chosen as a possible starting position for the stimulus.

For the training group, training and evaluation sessions were held on three consecutive days, with 24 h in between. An additional evaluation session without prior visual training was performed 1 week after the first day to investigate possible long-term effects of the training. Each daily session started with the VOG calibration procedure, followed by a 5-min pre-training pursuit evaluation with 60 step-ramp trials at the three different velocities (20 steps each). After a break of a few minutes, the visual training with the quasi-random paradigm started. The training consisted of two training sessions of 6 min each, with a

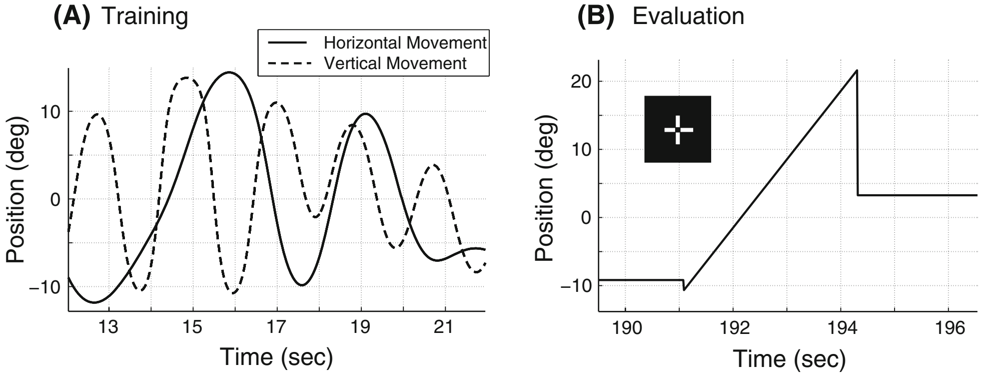


Fig. 1 **a** Training: *horizontal* and *vertical* movement of the training paradigm over time. **b** Evaluation: movement of the step-ramp stimulus with the target in the form of a *white cross* shown in the insertion. A Rashbass stimulus was used to measure pursuit velocity and gain

short pause in between. After another break, the VOG system was re-calibrated and the post-training pursuit evaluation followed. For the control group the same procedure was used, but with each training session replaced by a 6 min break.

Data analysis

Eye velocity was calculated by two-point differentiation of the eye position data in a trial-by-trial manner. For the calculation of open- and closed-loop gain we used eye velocity instead of initial eye acceleration, according to prior studies in this field (Fukushima et al. 1996; Bockisch et al. 2004). Since the sign of the acceleration typically does not change during the first 100 ms, any changes in the initial eye acceleration should be reflected in our definition of open loop gain. Noise was not critical, but in order to smooth the resulting eye velocity traces, we applied a moving average filter with 10 ms window size. Saccades were automatically detected and removed by using velocity thresholds. If the estimated eye velocity exceeded an error of 5°/s from the target velocity, the data in this area was overwritten with NaNs. Missing data, expressed by NaNs, were not interpolated to avoid falsified velocity values. Based on Bockisch et al. (2004) and Dubrovsky and Cullen (2002), open loop velocity was defined as the median eye velocity 80–100 ms after pursuit onset (see Fig. 2). Pursuit onset—or latency—was calculated by the intersection of two lines. A horizontal line was fit to the data from 50 ms before to 100 ms after the stimulus onset. Pursuit onset was then calculated as the intersection of this line with a regression line, which was fit to an 80 ms period of eye velocity data starting at the point where acceleration was at 80% of peak acceleration. Acceleration was again calculated by two-point differentiation of the velocity data. In this case, a moving average filter with 200 ms window size was used.

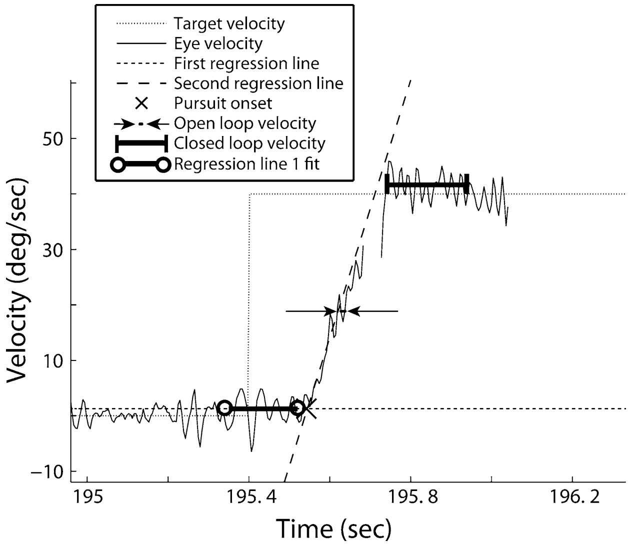


Fig. 2 Calculation of pursuit onset (latency), open- and closed-loop gains. The *graph* shows the target velocity step and pursuit response. The intersection of the *two regression lines* determines the onset of pursuit and therefore the latency. Open-loop velocity is calculated as median eye velocity 80–100 ms after pursuit onset and marked with the *two arrows*. Closed-loop velocity is defined as median eye velocity 200–400 ms after pursuit onset and indicated with a *thick bar* across the corresponding time interval

Closed-loop velocity was computed as the median eye velocity 200–400 ms after the calculated pursuit onset. Pursuit gain was defined as the ratio of measured eye velocity to current target velocity.

The fits were checked manually, and bad fits and trials with insufficient input data (e.g. due to saccades or blinks) were removed before statistical evaluation. If not indicated otherwise, values are given as mean ± standard deviation.

Statistical analysis was performed using Matlab (The Mathworks, Natick, USA). A test for normal distribution was performed by using a two-sample Kolmogorov–Smirnov test, Q–Q plots and histograms. For the actual pre-versus post-training comparison—as well as for the controls without training—the non-parametric Wilcoxon signed rank test for repeated measurements on single samples (two tailed, 5% significance level) was used. For the comparison of the control versus training groups we chose the non-parametric Mann–Whitney Wilcoxon rank-sum test (two tailed, 5% significance level).

Results

In the step-ramp paradigms used to evaluate pursuit performance, the subjects of both groups typically showed high gains for both open- and closed-loop smooth pursuit velocities. To see the effect of the stimulus velocity, we averaged the resulting closed-loop gains over all days, subjects and trials. In the training group, the average closed-loop gain was close to one for the lowest target velocity of 10°/s (1.03 ± 0.08). In some subjects eye velocity overshot target velocity in some trials. As expected, performance significantly declined at higher velocities: at 20 and 40°/s, the averaged mean closed-loop gain over all days, trials and persons was 0.97 ± 0.10 and 0.85 ± 0.16, respectively. The same findings were made in the control group, with the resulting values for both the training and the control group summarized in Table 1.

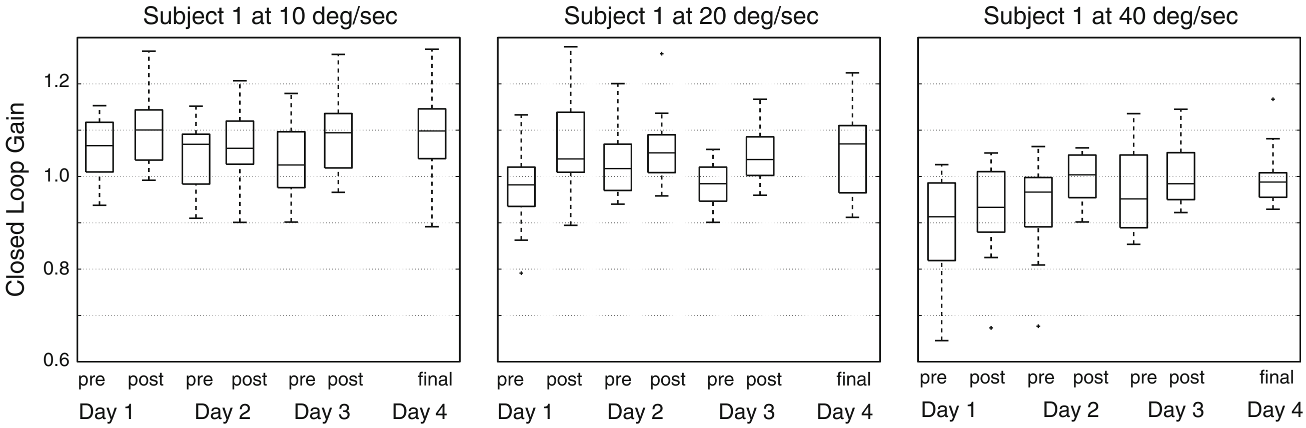
To demonstrate the effect of the training, Fig. 3 shows the closed-loop gain of one individual of the training group as a series of box plots.

One can clearly see the improvement of closed-loop performance with training: the trial-by-trial gains after the visual training sessions are consistently higher than the corresponding pre-training values. There is even evidence of a long term effect 5 days after the last training which can clearly be seen at target velocities of 20 and 40°/s. Another typical feature, which was also evident in the other subjects, is the decrease in variance at the highest target velocity after each training. In contrast to the closed-loop gain, the open-loop gain showed no significant improvement at any target velocity in either the target or the control group.

In Fig. 4 the results for all subjects in the training group are combined. The figure shows the open- and closed-loop mean gains of all subjects for each evaluation session, with the standard deviations as shaded areas. The white disruption of the graph indicates the break of 5 days between Day 3 and Day 8. The figure shows no significant change of open-loop performance for any target velocity. The most significant effect for all subjects can be seen at the highest target velocity for the closed-loop gain. There, the pre- to post-enhancement and the long term effect is apparent. For the closed-loop gain as a response to the 20°/s target velocity, a small effect is still visible. For the target moving

Table 1 The mean gains and standard deviation for each target velocity over all subjects, days and trials

Target velocity	Training group		Controls	
	Closed loop	Open loop	Closed loop	Open loop
10°/s	1.033 ± 0.077	0.783 ± 0.169	1.008 ± 0.081	0.762 ± 0.174
20°/s	0.974 ± 0.102	0.584 ± 0.155	0.933 ± 0.092	0.564 ± 0.116
40°/s	0.852 ± 0.155	0.389 ± 0.156	0.750 ± 0.158	0.334 ± 0.089


Subject 1 at 10 deg/sec

Subject 1 at 20 deg/sec

Subject 1 at 40 deg/sec

Fig. 3 Progress of closed-loop pre- and post-training gain for one individual subject. The measurement on Day 8—which was held 5 days after Day 3—was done without a training session prior to the evaluation. *Center line boxes* indicate the median and 25th and 75th percentiles, and the *error bars* indicate the measurement range

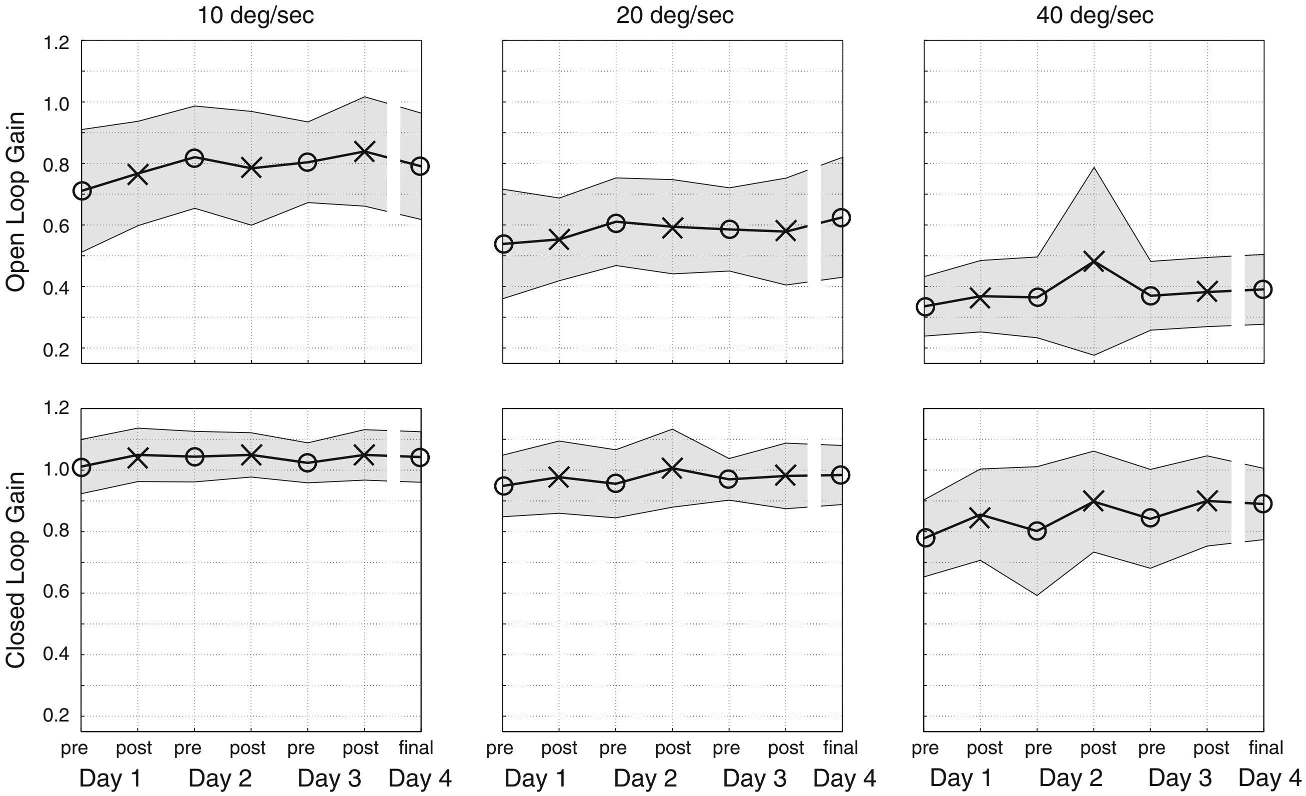


Fig. 4 Open- and closed-loop mean gains grouped by the different step-ramp target velocities. Gains of all subjects were calculated pre- and post-training with standard deviation shown in the *shaded areas*. The disruption in the graph indicates the 5-day break between Day 3 and Day 8. Pre-training data are indicated with "*o*", post-training data with "*x*"

at 10°/s there is no significant effect, although a slight enhancement of the mean performance immediately after training is still visible in the graph. No trend could be seen in the control group, at any stimulus velocity.

For 20 and 40°/s, Fig. 5 shows the closed-loop gains of all evaluation sessions (i.e. averaged over all sessions and over all subjects) of the training and control groups, normalized to the first evaluation (Day 1, pre). Since our measurements indicated a high inter-subject variability, we chose to show only the ratio of the gains instead of giving absolute values. As the data were not distributed normally (two-sample Kolmogorov–Smirnov test, $p = 0.031$ and graphical analysis via Q–Q plot and histogram), the statistical analysis was carried out using the Wilcoxon signed rank test. The statistical analysis of the data shown in Fig. 4 indicates that the training induced a clear and immediate enhancement of closed-loop performance for all target velocities ($p = 1.13 \times 10^{-7}$ for the comparison of all pre-training gains versus all post-training gains for all 3 days), with the clearest effect at the highest velocity tested ($p = 0.065$ at 10°/s, $p = 0.017$ at 20°/s and $p = 6.3 \times 10^{-6}$ at 40°/s). In contrast, the control group showed no such effect ($p = 0.292$ at 10°/s, $p = 0.984$ at 20°/s and $p = 0.369$ at 40°/s). Importantly, this training effect on the closed-loop performance also persisted: 5 days after the last training, the smooth pursuit performance averaged over all velocities was significantly higher than at the first evaluation ($p = 2.4 \times 10^{-4}$). Analyzing the performance for each individual velocity, the effect on smooth pursuit gain 5 days after the last training was significantly higher than the initial pursuit performance at 40°/s ($p = 0.002$). At the slower target velocities the effect was less pronounced and not significant. Again, there was no measurable effect in the control group for any of the tested target velocities.

For the open-loop gain, no pre- to post-training effect on pursuit performance could be measured ($p = 0.106$, 0.1055 and 0.091 for targets moving at 10, 20 and 40°/s, respectively). The same results hold for the evaluation of a long term effect which is rejected even more significantly ($p = 0.254$, 0.861 and 0.254 for 10, 20 and 40°/s).

The fact that the training effect is most significant at the highest velocity is not too surprising: at the lower velocities the gain was already close to unity, and thus could be little improved. This hypothesis is supported by comparing the high- and low-velocity gain values: at 40°/s, the gain was significantly lower than at 10°/s ($p = 0.002$, at Day 1-pre and Day 8). The difference was less pronounced, but still

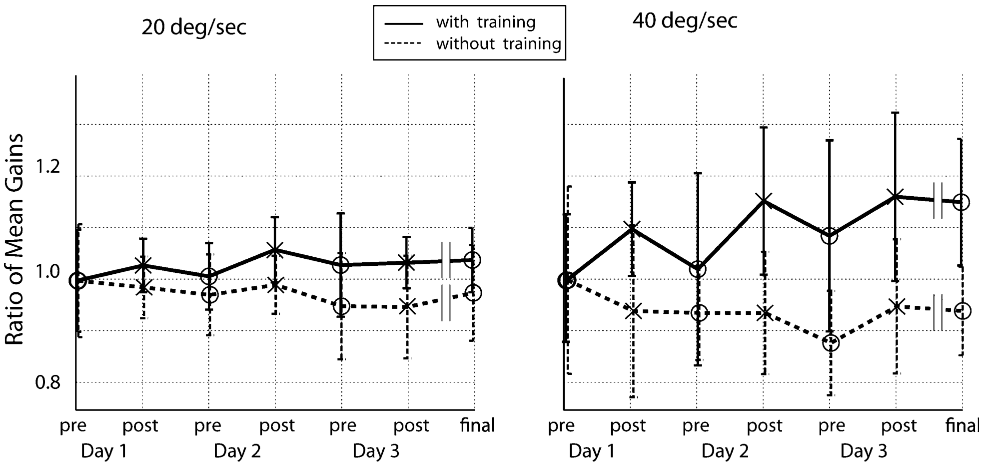


Fig. 5 Ratio of mean closed-loop gains of all subjects for the target moving at 20 and 40°/s. The ratio was calculated between the first pre-training evaluation on Day 1 to all other pre- and post-evaluations. The disruption of the graph between Day 3 and Day 8 again indicates the 5-day break between these two evaluations. The *error bars* for Day 1-pre indicate the standard deviation of the gain between subjects

significant when the 20°/s gains were compared to those at 10°/s ($p = 0.037$ and 0.0059 at Day 1-pre and Day 8, respectively).

A comparison of the normalized mean gains of training and control group on Day 8 with a Mann–Whitney Wilcoxon ranksum test yields the same result: the gain increase in the training group compared to the control group is significant at the highest target velocity ($p = 0.031$ at 40°/s), but not significant at lower velocities ($p = 0.121$ at 20°/s). This lack of significance may be due to the limited amount of subjects we had for our study: the power of the statistical test with our data is only 0.346, and at least 40 subjects would be needed to gain statistical significance at 20°/s.

Discussion

The results of our experiments show that even simple and short daily visual training can induce a sustained positive effect on smooth pursuit performance. Such training can be the tracking of a quasi-random target motion, obtained by the superposition of sine waves. We evaluated the effect of this visual training by carrying out experiments with 20 subjects—ten in the control group, ten in the training group. To evaluate possible contributions of perceptual learning from the testing procedure (Fahle 2005), the control group performed the same testing procedure as the training group, but had no training sessions in between. Our results showed short- and long-term smooth pursuit improvements in the training group, but no improvement in the control group. This finding fills a gap left by other investigations that have studied the plasticity of smooth pursuit and saccadic eye movements. Fukushima et al. (1996) have found immediate effects of smooth pursuit adaptation after visual training. They used velocity-enhancement and velocity-suppression paradigms for the training and step-ramp targets for the evaluation. In contrast, for our subjects the retinal slip during training is expected to be caused by a pursuit gain lower than unity for larger stimulus velocities. Correspondingly, our results only show no effect (for low stimulus velocities) or an increase in eye velocity (for large stimulus velocities) with training. Our results also confirm their finding that the training effect on eye movements depends on the parameter investigated. During the early phase of smooth pursuit (in the first 100 ms) there is not yet any feedback from the visual system, and the pursuit has to operate in an "open loop" fashion. Neither Fukushima nor we found any change of the eye movements during this period. After about 100 ms visual feedback becomes available, and pursuit can operate in "closed loop". This part of pursuit profits from the specific training, and showed significant improvement in our investigations. Other studies which focused on adaptive changes of early pursuit responses have shown that training that is aimed directly at modifying the initial eye acceleration can also modify the open loop component of pursuit eye movements (Chou and Lisberger 2004; Kahlon and Lisberger 1996). However, none of these studies asked if improvements in smooth pursuit performance persist, and other existing studies only investigated the effect of very intense, year-long training. Bockisch et al. (2004) showed that patients with bilateral vestibular loss have an increased quality of living when they have good smooth pursuit abilities. Their patients showed open- and closed-loop gains that were significantly higher than in controls, suggesting that the challenge of living with a deficient vestibular system can cause sustained enhancement of the pursuit system. Von Lassberg et al. (2012) demonstrated that after years of athletic training, the pursuit performance in professional gymnastics athletes is significantly better than in more sedentary, age-matched subjects. Recently, Ilg and Mack (2010) showed that players of computer games who play more than 2 h per day have shorter latencies of pro-saccades than non-players.

This also supports a study by Green and Bavelier (2003) who proposed that action video game playing may modify visual selective attention.

Our study targets an aspect not addressed by these previous investigations, and shows that the improvements of the closed-loop phase of pursuit eye movements elicited by short pursuit training sessions are persistent, and that these improvements accrue with repeated training. Five days after the last training there was still a highly significant effect on closed-loop performance for the highest target velocity tested (40°/s). Our finding that the effect was most pronounced at the highest target velocity indicates that the choice of the paradigm is important: the pursuit system has to be challenged in order to gain the best effect of learning. This is not too surprising as closed loop gain was already nearly one at the target speed of 10°/s and could not be improved further. The challenge to the pursuit system is also reflected by the increased standard deviation with higher velocities, indicating higher inter-subject variability in pursuit performance.

As in previous studies, we tested smooth pursuit performance by using a step-ramp paradigm (Rashbass 1961). It is also possible to test pursuit performance with more sinusoidal-style paradigms, but they have the disadvantage of predictive effects (Barnes 2008). In our setup, prediction is precluded by using randomized velocities, movement directions and starting positions of the step-ramp target for the evaluation paradigms. We think that using another paradigm for training and evaluation shows that improvements in smooth pursuit performance do not depend on the precise training paradigm, which is consistent with the findings of Bockisch et al. (2004) and von Lassberg et al. (2012). This is supported by the results from the control group, who underwent only the same evaluation procedures but had no visual training.

One obvious question regarding our results is which neural substrate underlies the observed changes. As smooth pursuit is a conscious, non-reflexive movement, the answer to this question is remarkably difficult. For reflexive eye movements like the vestibular ocular reflex (VOR) or saccades, adaptive changes have already been well studied and are reasonably well understood. They typically involve cerebellar as well as brainstem structures (see Tian et al. 2009; Pelisson et al. 2010) for recent reviews about adaptation of saccadic eye movements (Boyden et al. 2004) for the plasticity of the VOR and (Schubert and Zee 2010) for both the saccadic and VOR oculomotor system). The underlying coding and plasticity mechanisms in the VOR are thought to be of sufficient richness to enable adaptive learning by multiple sensory inputs. In recent review articles Boyden et al. (2004) and Burke and Barnes (2008) summarized that the neuronal mechanisms for the more position-dependent saccadic responses are located in the frontopolar region, compared to the rather velocity dependent pursuit mechanisms in the dorsolateral prefrontal cortex, an area thought to also play a role during 'executive processes' and therefore referred to as 'central executive' (Baddeley 1992). Unlike the VOR, smooth pursuit eye movements are not reflexive movements and it is still unclear which neurological structures underlie adaptive changes after training or learning for smooth pursuit. As suggested by Barnes (2008), we hypothesize that improved attention, believed to be mediated via the proposed central executive, is one of the driving factors in the observed improvements in smooth pursuit performance, at least for the short term effects measured. This would be consistent with the results of (Green and Bavelier 2003) that showed that action video gaming alters aspects of visual attention in comparison to non-players. Another interpretation consistent with the results of our adaptation training is that there are two independent and different subsystems of the visual system: one for fixation and one for smooth pursuit responses (Leigh and Zee 1999): improved attention might facilitate the switch from the fixation system to the pursuit system, thereby improving the observed smooth pursuit performance.

We excluded possible contributions by perceptual learning (Fahle 2005) in our study through the control experiments. The fact that the control group showed no changes in eye movement performance over the experiment verifies that the measured improvement of smooth pursuit performance is not due to the evaluation paradigm, but caused by the different training stimulus and therefore more generalized. This is a finding that has also been indicated by the study of Green and Bavelier (2003) again, showing a generalization of learning after playing action computer games to other tasks involving visual attention processing.

The goal of our study was to investigate whether learning effects for the smooth pursuit system can be achieved with short training sessions and if such effects persist. Even with our relatively small number of subjects, our results clearly confirm these two hypotheses for the highest velocity tested. Results were less pronounced for the 10 and 20°/s gains. Since the inter-subject differences in the smooth pursuit gains are significant (Fig. 4), a larger sample size would be required to give firm boundaries for the magnitude of the learning effect. Nevertheless, even with our limited sample size the gain increase 5 days after the last training was significantly raised at 40°/s, not only within each subject but also comparing the training group with the control group.

Our findings strongly support the idea of visual training as a rehabilitation treatment for patients with chronic or recurrent vestibular problems, and (Loader et al. 2007) has already demonstrated that training of the visual system can improve balance. The training used in our setup is cheap and simple, and could even be done at home in front of a standard computer monitor. For routine applications we suggest employing a more varied stimulus than the one used here, as preliminary experiments that we have performed with patients indicated that the pursuit of a white cross on a black background quickly exhausts the interest of the patients.

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