Eye movement training is most effective when it involves a task-relevant sensorimotor decision

Jolande Fooken[1,2]*, Kathryn M. Lalonde[1,2], Gurkiran K. Mann[1] & Miriam Spering[1,2,3,4]

[1] Dept. Ophthalmology & Visual Sciences, University of British Columbia, Vancouver, Canada

[2] Graduate Program in Neuroscience, University of British Columbia, Vancouver, Canada

[3] Center for Brain Health, University of British Columbia, Vancouver, Canada

[4] Institute for Computing, Information and Cognitive Systems, University of British Columbia, Vancouver, Canada

*Corresponding author's address:
Visual Performance and Oculomotor Mobility Lab
Blusson Spinal Cord Centre
818 W10th Avenue
Vancouver, BC V5Z 1M9 Canada
Email: fooken@cs.ubc.ca

Abstract

Eye and hand movements are closely linked when performing everyday actions. We conducted a perceptual-motor training study to investigate mutually beneficial effects of eye and hand movements, asking whether training in one modality benefits performance in the other. Observers had to predict the future trajectory of a briefly presented moving object, and intercept it at its assumed location as accurately as possible with their finger. Eye and hand movements were recorded simultaneously. Different training protocols either included eye movements or a combination of eye and hand movements with or without external performance feedback. Eye movement training did not transfer across modalities: irrespective of feedback, finger interception accuracy and precision improved after training that involved the hand, but not after isolated eye movement training. Conversely, eye movements benefited from hand movement training or when external performance feedback was given, thus improving only when an active interceptive task component was involved. These findings indicate only limited transfer across modalities. However, they reveal the importance of creating a training task with an active sensorimotor decision to improve the accuracy and precision of eye and hand movements.

Keywords: eye movements, hand movements, motion prediction, interception, perceptual learning, training, feedback

Eye movement training is most effective when it involves a task-relevant sensorimotor decision

Vision and eye movements guide most of our everyday actions. When we reach for an object, our gaze is shifted to the target long before the hand. This predictive gaze behavior serves to gather information about object identity and location, and marks future contact points for hand and fingers (Smeets, Hayhoe, & Ballard, 1996; Land, Mennie, & Rusted, 1999; Johansson, Westling, Bäckström, & Flanagan, 2001). When performing everyday actions, eye movements reflect the detailed evolution of the hand movement and the requirements of the task (Hayhoe & Ballard, 2005; Hayhoe, 2017). Gaze also leads the target when we interact with moving objects, such as catching a ball, and thus reveals knowledge of the future target path (Diaz, Cooper, Rothkopf, & Hayhoe, 2013). Moreover, eye movements can be made predictively, for example during an occlusion interval, and scale with visual target properties such as acceleration (Bennett, Orban de Xivry, Barnes, & Lefèvre, 2007). In this context, it has been shown that more accurate tracking eye movements (smooth pursuit) result in better prediction of an object's trajectory (Bennett, Baures, Hecht, & Benguigui, 2010; Spering, Schütz, Braun & Gegenfurtner, 2011). Tracking a moving object with smooth pursuit is also associated with higher accuracy in hand movement planning (Leclercq, Blohm, & Lefèvre, 2013) and execution (Fooken, Yeo, Pai & Spering, 2016). It is important to note, however, that pursuit does not necessarily have to be aligned with the target until the moment of interception (Brenner & Smeets, 2011; López-Moliner & Brenner, 2016; de la Malla, Smeets, & Brenner, 2017). Rather, it seems that the initiation of pursuit and subsequent combination with saccades is sufficient to enable successful interception. Correspondingly, ball sport athletes commonly track the ball briefly using a combination of eye and head movements and then saccade to an anticipated bounce or contact location (Bahill & LaRitz, 1984; Diaz, Cooper, Rothkopf, & Hayhoe, 2013; Mann, Spratford, & Abernethy, 2013). Such a combination of tracking or gaze holding and prediction in eye movement behavior is now considered a basic skill underlying superior athletic performance (Bahill & LaRitz, 1984; Land & McLeod, 2000; Mann et al., 2013; Uchida, Kudoh, Higuchi, Honda, & Kanosue, 2013; Vickers, 2016).

Here we probe the relation between eye and hand movements in a rapid interception task using a perceptual training paradigm. First, we investigate whether eye-movement training enhances the ability to perform untrained goal-directed hand movements. Second, we assess whether eye movement training is sufficient to enhance hand movements, or whether it would be more effective if it was combined with hand movement training.

The idea of transfer across modalities—from eye to hand—is based on the known tight link between eye and hand movements. On one hand, such transfer of training does not readily occur in perceptual or motor learning. For example, one of the hallmarks of perceptual learning is its specificity, i.e., lack of transfer to untrained tasks, visual locations, features, or across modalities (Polat & Sagi, 1994; Fahle, 2005). On the other hand, specificity depends on stimulus characteristics and task requirements. Transfer of perceptual learning from one location to another has been observed when the second location was previously sensitized via training an irrelevant task at that location (Xiao et al., 2008) or when the same stimuli were used (Porat & Zohary, 2016). Transfer across tasks, for example, from Vernier acuity and contrast detection to Snellen acuity, has been observed in patients with amblyopia (Levi & Li, 2009) and college baseball players (Deveau, Ozer, & Seitz, 2014), who even seem to improve on-field performance following such training (see also Faubert, 2013). The broadest transfer of perceptual learning beyond the trained task has been found after training with action video games (Green & Bavelier, 2012; Li, Chen, & Chen, 2016), resulting in improved selective attention (Green & Bavelier, 2003) and spatial resolution across the visual field (Green & Bavelier, 2007). Transfer of learning across modalities, from perception to eye movements, is possible if the task requires responses with similar underlying processing mechanisms. Szpiro, Spering, and Carrasco (2015) trained observers in a motion discrimination task during fixation and found generalization to untrained smooth pursuit eye movements. Transfer of learning has also been observed in other modalities, such as the somatosensory system: tactile perceptual learning can transfer to untrained fingers (Dempsey-Jones, Harrar, Oliver, Johansen-Berg, Spence, & Makin, 2016).

To address the question whether eye movement training is sufficient to enhance hand movement accuracy, we define and measure performance improvements in hand movement accuracy following isolated training (eye movements are trained, hand is not trained) or combined training (eye and hand movements are trained simultaneously). In an effort to address a bidirectional relation between eye and hand movements, we also investigate the effect of isolated or combined training on eye movement accuracy and precision. A comparison of effects of different training protocols will allow us to evaluate whether eye movement training alone is sufficient to improve the eye, or whether there are added benefits of involving the hand in training, indicating transfer.

We assessed participants in a motion prediction task that required rapidly intercepting a moving object with the hand. In this task, participants viewed a target moving along a curved trajectory—akin to a lateral view of a batted baseball. Importantly, the target was shown only briefly, and participants had to extrapolate its motion trajectory before intercepting it in a dedicated area on the screen. Ultra-short target presentation durations make this task difficult (Fooken et al., 2016) and therefore suitable for a training paradigm. Eye and hand movements were recorded simultaneously. Testing and training with different training protocols occurred over a period of five consecutive days; we also assessed the longer-term retention of learning in a follow-up session one week after training. Some of the training protocols involved an active movement towards the assumed target position and external performance feedback on whether the eye or hand successfully reached the target. Performance feedback is widely considered an important component in training across modalities (Swinnen, 1996; Herzog & Fahle, 1999; Gray, 2009; Wolpert, Diedrichsen, & Flanagan, 2011; Sigrist, Rauter, Riener, & Wolf, 2013). It might accelerate learning (Fahle & Edelman, 1993; Werner & Bock, 2007) and facilitate transfer (Salmoni, Schmidt, & Walter, 1984; Swinnen, Verschueren, Serrien, & Bogaerds, 1997; Deveau, Ozer, & Seitz, 2014; Tanaka & Watanabe, 2017). We manipulated external performance feedback to investigate and compare feedback effects on eye and hand movement (see below, Hypotheses).

Materials and Methods

Participants

We recruited 50 right-handed undergraduate students (mean age = 24.2 years; *SD* = 3.5; 29 female) with corrected-to-normal visual acuity and no history of disease interfering with normal eye movement function. The experimental protocol adhered to the Declaration of Helsinki and was approved by the UBC Behavioral Research Ethics Board. Participants gave written informed consent prior to participation and were unaware of the purpose of the experiment. Each participant was randomly assigned to one of five groups (*n* = 10 each): four training groups that were tested at least five times and one control group that was tested at least twice (see **Table 1**). Sample size per group is comparable to other studies investigating training effects on eye or finger movements (Porat & Zohary, 2016; Dempsey-Jones et al., 2016). Remuneration was $8 per hour for each session; a bonus of $20 was paid upon completion of all five sessions. All 50 observers completed the study, and 41 of them returned for the follow-up session one week later ($10 remuneration).

- Table 1 here -

Visual stimuli and apparatus

Stimuli, apparatus, and task were based on methods developed in Fooken et al. (2016), and are reproduced here for the reader's convenience. Observers had to track and intercept a briefly presented, small, black Gaussian dot with diameter 2 degrees of visual angle (°), shown at a luminance of 5.4 candela per meter squared (cd/m^2). The stimulus moved across a uniform gray background equally divided into a lighter gray "tracking zone" on the left (35.9 cd/m^2) and a darker gray "hit zone" on the right (31.5 cd/m^2; **Fig. 1a**). The physical trajectory of the target was simulated to be the natural flight of a batted baseball. Visual stimuli were back-projected using a PROPixx video projector (VPixx Technologies, Saint-Bruno, QC, Canada) with a refresh rate of 60 Hz and a resolution of 1280 (H) × 1024 (V) pixels. Observers sat at a distance of 46 cm from the screen with their head supported by a chin and forehead rest. The screen was a 44.5 cm × 36 cm translucent display consisting of non-distorting projection screen material (Twin White Rosco screen, Rosco Laboratories, Markham, ON, Canada) clamped between two glass panels and fixed in an aluminum frame. Stimulus display and data collection were controlled by a Windows PC with an NVIDIA GeForce GT 430 graphics card running Matlab 7.1 and Psychtoolbox 3.0.8 (Brainard, 1997; Pelli, 1997).

- Figure 1 here -

Procedure, task and design

Testing sessions. Observers were tested before training (pre-test) and after training (post-test and follow-up test) using the following procedure and task (**Fig. 1b**): Each trial began with fixation on a stationary ball presented 14° to the left from screen center; fixation duration was randomized (500-700 ms). The ball then moved to the right at one of three speeds (25, 30, 35°/s) and disappeared after a short presentation duration (100, 200, or 300 ms) before reaching the hit zone (see **Fig. 1a**). Speed and presentation duration were randomized within each block of trials. Observers were instructed to track the ball smoothly with their eyes, to continue to track it after it disappeared, and to intercept it with their index finger at an assumed position anywhere within the hit zone. Interceptions were always made in the ipsilateral (right) half of the screen and observers returned their hand to a table-fixed resting pad after each trial. Feedback on manual interception performance was provided at the time of interception; a red dot indicated interception location and a black dot indicated true target position (**Fig. 1b**). Performance feedback was visible for 500 ms; the next trial started in immediate succession. Each pre- or post-testing session (162 trials) took approx. 20 minutes.

Training sessions. Training protocols (groups 1-4; days 2-4) differed with regard to response modality (eye alone or combined eye-hand) and visual feedback (**Table 1; Fig. 1c**). Groups 1 and 2 did not move their hand during training. Group 1 was instructed to track the target with their eyes into the hit zone; the target never reappeared, and observers received no performance feedback. Group 2 was asked to track the target and to actively intercept it with their eyes. To be recognized as final eye position ("hit" or "intercept"), observers had to hold their gaze within a 1.4 degree radius of the assumed target position in the hit zone for 200 ms. They received feedback about where the target was relative to their eye: a red dot indicated their final eye position, and a black dot showed true target position. Observers in groups 3 and 4 were asked to track the target with their eyes and to intercept it with their finger, just as they did during testing. Group 3 received no feedback (only interception position, not true target position, was shown) and group 4 received the same full performance feedback as during testing. Training sessions included three blocks of 162 trials each (486 trials total) and took approx. 60 minutes to complete. Group 5 served as a control and received no training; these participants were only tested twice and did not come into the lab on training days.

Eye and hand movement recordings and analysis

We recorded right eye position with a video-based eye tracker (tower-mounted Eyelink 1000, SR Research Ltd., Ottawa, ON, Canada) at a sampling rate of 1000 Hz. At the start of each block of trials, the measurements were calibrated by asking observers to fixate on a small visual target appearing successively at nine different locations on the screen; this procedure was repeated for validation. All data were analyzed off-line using custom-made routines in Matlab for the detection of saccades and pursuit onset (Fooken et al., 2016). Saccades were excluded from pursuit analysis and analysed separately. We computed relative eye velocity (calculated as gain: frame-by-frame eye velocity divided by target velocity in the interval 140 ms after pursuit onset to interception) as the parameter defining pursuit quality. We also computed the cumulative amplitude of catch-up saccades, i.e., the total distance covered by saccades. To investigate how closely the eye landed relative to the final position of the target at the end of the trial we analyzed the interception error of the eye. For this measure, we defined the target position, p_{tar}, and the final eye position p_{eye} at the time the trial finished. The trial finished either when the target was intercepted manually (pre- and post-test; groups 3 and 4), the target was intercepted with the eyes (group 2), or the target reached the end of its trajectory (group 1). Eye interception error (or accuracy) was then calculated as the Euclidean distance $d_{eye} = \|p_{tar} - p_{eye}\|$.

During all testing sessions, and during training sessions that involved the hand (groups 3 and 4), movements of observers' right index finger were tracked with a magnetic tracker (3D Guidance trakSTAR, Ascension Technology Corp., Shelburne, VT, USA) at a sampling rate of 240 Hz. A lightweight sensor was attached to the observer's fingertip with a small Velcro strap. Calibration of measurements obtained with the trakSTAR relied on a 5-point procedure in which observers were asked to point to the location of a visual target appearing successively at five locations with their index finger and keep their finger at this location until the next target appeared. This procedure immediately followed eye tracker calibration at the start of each trial. We recorded the 2D finger interception position in x- and y-screen-centered coordinates for each trial. To analyse manual interception accuracy, we first defined the finger hit position, p_{finger}, as the 2D position of the finger when it first makes contact with the screen. The target position at that time is denoted as p_{tar}. Interception accuracy is the interception error, calculated as the Euclidean distance $d_{finger} = \|p_{tar} - p_{finger}\|$. We also analysed interception precision, defined as the statistical variance, indicating spatial variability of x- and y-interception positions. All trials were manually inspected, and those with eye blinks (4.3% of all trials), hand movement onset prior to target onset (1%), or undetected finger end position (2%) were excluded from further analysis.

Hypotheses and statistical analyses

Hypotheses are graphically presented in **Figure 2**. First, we expected that movement accuracy would improve in all training groups as compared to the control group. This improvement might be limited to the trained modality, i.e., hand movement accuracy will increase when training involves moving the hand and eye movement accuracy will increase after training that involves the eye (Hypothesis 1a; **Fig. 2a**). Alternatively, the improvement might transfer across modalities, i.e., hand movement accuracy will increase after eye movement training and eye movement accuracy will increase after hand movement training (Hypothesis 1b; **Fig. 2a**). Second, we expected that external performance feedback based on an active interceptive movement might boost movement accuracy for each modality (Hypothesis 2; **Fig. 2b**). Alternatively, if transfer was found (Hypothesis 1b) feedback might enhance performance across modalities.

- Figure 2 here -

Differences between groups, and the hypothesis that each training group improved within the given response modality more than the control group, were examined using one-way ANOVA with factor *group*. Inter-group differences were examined using a post-hoc Dunnett's test to account for potential dependencies in multiple comparisons between each training group and the control group (Dunnett, 1955). With n – k degrees of freedom (sample size minus number of groups), $\alpha = 0.05$, five groups, and a sample size of $n = 10$ per group, the critical value above which a Dunnett's test would be significant is $t = 2.89$. We also compared training groups with regard to response modality and whether or not feedback was given using repeated-measures ANOVA with factors *modality* and *feedback*. Changes across training days were investigated with repeated-measures ANOVA with factor *day*. In all groups and sessions, speed and presentation duration were varied to increase stimulus uncertainty. Based on previous studies using the same paradigm, we expected that these stimulus conditions would systematically affect eye and hand movements (Fooken et al., 2016; Kreyenmeier, Fooken, & Spering, 2017), and we replicate and report those results here. Effects of speed and presentation duration were analysed using repeated-measures ANOVA with factors *speed* and *duration*; this analysis was conducted on data averaged across training groups for the pre-test. However, we had no specific hypotheses regarding interactions between training groups and stimulus conditions, and thus pooled across speeds and presentation durations when testing our main study hypotheses. Statistical analyses were conducted in IBM SPSS Statistics Version 24 (Armonk, NY, USA).

Results

Our results focus on the effects of training on eye and hand movement accuracy (Hypothesis 1, **Fig. 2a**) and describe how performance changed from pre-test to post-test. We also consider the role of external feedback in task versions requiring active interception (Hypothesis 2, **Fig. 2b**), and day-to-day improvements across training days.

Effects of target properties on eye and hand movements

We varied speed and presentation duration—two variables that can be expected to strongly influence eye and hand movements. Replicating previous results (Fooken et al., 2016), pursuit was more accurate when the target was presented for a longer duration and when it moved at a slower speed: relative eye velocity increased with increasing presentation duration ($F(2,98) = 115.4$, $p < .001$, $\eta^2 = .70$) and with decreasing speed ($F(2,98) = 247.9$, $p < .001$, $\eta^2 = .84$). Manual interceptions were most accurate (smallest interception error) when the target was presented for a longer duration ($F(2,98) = 58.3$, $p < .001$, $\eta^2 = .54$) and when it moved at a medium speed ($F(2,98) = 38.53$, $p < .001$, $\eta^2 = .44$), indicating a speed-range effect (see Fooken et al., 2016).

In general, observers tended to intercept early in the hit zone and close to the medium-speed target trajectory, in line with a speed-range effect. These patterns were observed across all groups, despite high individual variability in interception strategy (e.g., early vs. late in the hit zone). **Figure 3** shows 2D interception positions during pre- and post-test for four representative observers; two observers from the control group, for whom we would expect the smallest performance increase, and two from group 4 (eye-hand training with feedback), for whom we would expect the largest performance increase.

-Figure 3 here-

Whereas absolute interception position and timing (later interceptions were made further into the hit zone) differed between individuals, they did not differ significantly between groups. This observation was confirmed using a multivariate ANOVA with *group* as fixed factor, yielding no significant group effects on differences between x-interception position ($F(4,45) = 1.71$, $p = .16$, $\eta^2 = .13$) or y-interception position ($F < 1$) in pre-test versus post-test. Our main analyses therefore focus on interception accuracy and precision, rather than on absolute position.

Training the hand enhanced hand movement accuracy and precision irrespective of external feedback

We calculated finger interception error, i.e. the 2D distance between finger and target end position at time of interception, to evaluate hand movement accuracy. Interception error was overall smaller after training as compared to before training in all groups (**Fig. 4a**). The largest percentage improvements can be seen in groups that trained while using their hand (**Fig. 4b,c**). These observations were confirmed by significant comparisons (Dunnett's *t*) between hand-training groups with the control group (group 3: $p = .05$, Cohen's $d = 1.2$; group 4: $p = .02$, $d = 1.41$), implying that training the hand in a manual interception task improved interception accuracy. Performance in the eye-training groups also improved as compared to the control group, but these changes were non-significant (group 1: $p = .53$, $d = 0.27$; group 2: $p = .27$, $d = .65$), reflected in an overall non-significant effect of the factor *group* ($F(4,45) = 2.2$, $p = .08$, $\eta_p^2 = .16$). These results indicate that hand movement accuracy only improved when the hand was engaged during training, whereas isolated eye movement training did not benefit the hand.

Notably, the interception performance level achieved after training remained stable or continued to increase one week later (see **Fig. 4d**). A repeated-measures ANOVA with within-subjects factor *time* (post vs. week test) and between-subjects factor *group* revealed a significant main effect of *time* ($F(1,35) = 5.93$, $p = .02$, $\eta^2 = .15$) and a significant *group* × *time* interaction ($F(4,35) = 2.97$, $p = .03$, $\eta^2 = .25$). Note that these statistics are based on observers who participated both in the post-test and in the week test ($n = 41$). Hence, they do not exactly match post-test means shown in **Figure 4b** for $n = 50$.

- Figure 4 here -

Whereas feedback did not modulate hand movement accuracy after training—no significant main effect of *feedback* on post-test performance (see **Fig. 4c**), and no *feedback* × *modality* interaction (all $F < 1$)—it did affect the time course of learning. **Figure 4b** shows improvements in interception accuracy relative to pre-test for each day. When feedback was given (group 4), interception accuracy increased across training days, saturated on day 3, and remained stable during post-test. When no feedback was given and observers had no knowledge of the target end position (group 3), interception accuracy decreased across training days, indicating that observers hit further away from the target in the absence of feedback. Performance in this group recovered during post-test when observers received feedback, reaching the same performance level as the group that had received feedback throughout training. These observations were confirmed by a repeated-measures ANOVA with factors *feedback* and *day*, yielding a significant main effect of *day* ($F(5,65) = 7.3$, $p < .001$, $\eta_p^2 = .36$) and a *feedback* × *day* interaction ($F(5,65) = 4.13$, $p = .003$, $\eta_p^2 = .24$). In sum, hand movement accuracy increased significantly following training that involved the hand. These improvements occurred irrespective of feedback, even though feedback modulated performance during training days.

It is noteworthy that performance increased even in the absence of any training (see control group data in orange in **Fig. 4**), posing the question whether the pre-test alone might have been sufficient to provide full and extensive training of the task. We investigated this possibility by analysing average interception error during the pre- and post-test in bins of 9 trials. **Figure 5** shows average binned interception errors for two groups—group 5 (no training) as the group that improved the least (**Fig. 5a**), and group 4 (eye-hand training with feedback) that improved the most (**Fig. 5b**). For both groups, interception error decreased during the first half of the pre-test, and then remained stable at a level of around 3 deg on average across all speeds. Even though the control group's performance improved at the start of the post-test in the absence of training, overall interception error was higher ($M = 2.4 \pm 0.13$ deg) than for the eye-hand training group ($M = 2.1 \pm 0.16$ deg), indicating that additional training was useful. This group continued to improve on training days, and reached an overall higher level of accuracy. Most importantly, neither group achieved ceiling performance at any time.

-Figure 5 here-

Finally, we investigated effects of training on interception precision, the spatial variability of x- and y-interception positions. **Figure 6** shows mean variance for each group before and after training and reveals large improvements in precision for the four training groups, especially along the horizontal axis (timing; i.e., how far into the hit zone observers intercepted; see **Fig. 3**). The control group also improved, but to a much smaller extent (**Fig. 6e**), maintaining relatively large spreads in horizontal and vertical directions (see also **Fig. 3a**).

-Figure 6-

Training the eye differentially enhances eye movement performance

Training effects on eye movements were quantified by calculating two main performance measures: interception error of the eye (i.e., eye position relative to final target position), and relative eye velocity (i.e., eye velocity relative to target velocity).

Similar to the pattern observed for manual interception error, the eye interception error decreased with training (main effect of *group* on accuracy improvement in post-test relative to pre-test; $F(4,49) = 2.96$, $p = .03$, $\eta_p^2 = .21$; **Fig. 7a**). When no feedback was given and observers had no knowledge of the target end position (group 1), eye interception accuracy decreased across training days (**Fig. 7b**). Performance in this group recovered during post-test when observers received feedback, reaching the same performance level as the group that had received feedback throughout training. However, we observed no significant overall inter-group differences due to large improvements in the control group (**Fig. 7c**). Across all groups, observers' final eye and hand positions were closely linked, indicating that observers pointed where they looked, within 1.9 ± 0.32 deg in the pre-test, and 1.5 ± 0.25 deg in the post-test.

-Figure 7 here-

Figure 8 shows mean eye velocity profiles for all test and training days for each group. Observers commonly initiated smooth pursuit in anticipation of the predictable motion direction; the frequency of occurrence of these anticipatory movements increased with exposure to the task (compare pre- and post-test velocity values at time 0, when the target started moving). At around 100-150 ms after target onset eye velocity increased rapidly, but never reached target speed, decreasing again after reaching a peak at around 300 ms. Pursuit's transient nature in this task is due to limited target presentation duration (100-300 ms), and the peak at 300 ms indicates that observers attempted to maintain pursuit up to the maximum visible target duration. Accordingly, relative eye velocity (gain) values were on average 0.25 ± 0.11. The eye velocity profiles reveal an increase in eye velocity from pre-test to post-test in training groups 2-4 (compare colored dotted and dashed lines in panels b-d). In these groups, performance also improved across training days from day 1 to day 3 (compare light and dark grey lines). By contrast, group 1 showed only a slight increase, and the control group showed no increase in eye velocity.

- Figure 8 here -

We quantified the observed effects of training by calculating relative eye velocity, i.e. the mean of the ratio of eye versus target velocity at each time frame between 140 ms after onset to time of interception, as a measure of eye movement accuracy. Training effects emerged early during the pursuit response and built up over time, reaching a peak at around 250 ms after stimulus onset, just before the eye started to decelerate. Correspondingly, relative eye velocity increased up to 20% in the training groups, whereas the control group's relative velocity slightly decreased from pre to post-test (**Fig. 9a-c**). These findings were confirmed by a significant main effect of *group* on relative velocity improvement in post-test in comparison to pre-test ($F(4,49) = 3.65$, $p = .01$, $\eta_p^2 = .25$). Similar to what we observed for hand movement accuracy, eye movement performance differences were significant in both hand-training groups regardless of feedback (group 3: $p = .01$, $d = 1.32$; group 4: $p = .006$, $d = 1.16$). Accordingly, we found no main effect of *feedback* on post-test relative velocity in training groups ($F(1,36) = 1.88$, $p = .18$, $\eta_p^2 = .05$), and no *feedback* × *modality* interaction ($F(1,36) = 1.82$, $p = .19$, $\eta_p^2 = .05$).

- Figure 9 here -

Eye movement improvements were also significant in the eye training group that received feedback ($p = .005$, Cohen's $d = 1.63$), but not in the eye training group without feedback ($p = .13$, $d = .81$). Again, feedback modulated the time course of learning (compare green lines in **Fig.**

9b). This observation was confirmed by a main effect of *feedback* on relative eye velocity for the two eye-movement training groups ($F(1,18) = 17.21$, $p = .001$, $\eta_p^2 = .49$), but not for the hand-training groups ($F < 1$). This differential modulatory effect of feedback on eye and hand movement training was reflected in a significant *feedback* × *modality* interaction ($F(2,36) = 25.07$, $p < .001$, $\eta_p^2 = .59$) during training days, and across all testing and training days ($F(1,10) = 6.01$, $p = .03$, $\eta_p^2 = .38$).

Similar to what we observed for hand movement performance, eye accuracy remained unchanged compared to post-test when tested one week later (see **Fig. 9d**). A repeated-measures ANOVA with within-subjects factor *time* (post vs. week test) and between-subjects factor *group* revealed no effect of *time* ($F(1,35) = 1.58$, $p = .22$, $\eta^2 = .04$) and no *group* × *time* interaction ($F < 1$). Again, these statistics are based on subjects who participated in the week test ($n = 41$), resulting in the difference to post-test data shown in **Figure 9b** for $n = 50$. In sum, eye movement accuracy increased significantly either when training involved the hand, or when external performance feedback was given, as was the case in task versions that involved a sensorimotor decision.

It is important to note that performance differences between the two isolated eye training groups (**Fig. 9b,c**) could result either from the fact that only one of these groups received external performance feedback, or from differences in eye movement behaviour. Whereas group 1 merely tracked the target, group 2 was asked to intercept with their eyes, triggering a goal-directed movement at the assumed target position. As a result of this instruction, observers in groups 1 and 2 produced eye movement patterns that differed both qualitatively and quantitatively, resulting in overall higher eye interception accuracy in group 2 (see also **Fig. 7b**). Observers in group 1 tracked the target for longer periods of time, using a combination of smooth pursuit and saccadic eye movements (see example in **Fig. 10a,c**), whereas observers in group 2 made an early saccadic eye movement towards the target, thus terminating the trial (**Fig. 10b,d**). Congruent with these observations, observers in group 1 initiated their final saccade on average 500 ms later than group 2 (latency group 1: $M = 1169 \pm 39$ ms; group 2: $M = 503 \pm 12$ ms). Moreover, observers in group 1 made on average twice as many saccades as compared to group 2 (group 1: $M = 4.3 \pm 0.24$; group 2: $M = 2.4 \pm 0.14$), resulting in a larger cumulative saccade amplitude (group 1: $M = 31 \pm 1.9$ deg; group 2: $M = 15 \pm 0.5$ deg). These results indicate that performance differences between both groups are likely modulated by differences in task, rather than the fact that external performance feedback was given.

-Figure 10 here-

Discussion

This study investigates under which circumstances perceptual-motor learning transfers across modalities, and the mechanisms underlying performance improvements in eye and hand movements. Using a motion prediction task and comparing five different types of training, we report three key findings. First, eye movement training does not transfer to hand movements, despite known close links between both modalities in tasks that involve goal-directed hand movements. Second, eye movements improve most when training involves an interceptive movement (either eye or hand). Third, external performance feedback has relatively little influence on training outcome.

Eye movement training does not transfer to hand movements

Eye movements are usually made spontaneously when observers engage in visually-guided manual tasks such as reaching, grasping, pointing or hitting. Eye and hand movements are spatially and temporally coordinated: gaze leads the hand by up to 1 second (Ballard et al., 1992; Smeets et al., 1996; Sailer, Flanagan, & Johansson, 2005; Land, 2006), and gaze locations are anchored to future contact points on the target, indicating strong spatial coupling (van Donkelaar, Lee, & Gellman, 1994; Neggers & Bekkering, 2000; Gribble, Everling, Ford, & Mattar, 2002; Brenner & Smeets, 2011; Cesqui, Mezzetti, Lacquaniti, & d'Avella, 2015; Vazquez, Federici, & Pesaran, 2017). Many of these studies have focused on the saccade-to-reach relationship. Using the same motion prediction task as in the current study, we recently extended these findings to smooth pursuit, revealing a close relationship between the accuracy of pursuit and the accuracy of manual interceptions (Fooken et al., 2016). This link was closest at the time of interception, indicating a common spatiotemporal framework for the control of smooth pursuit and interceptive hand movements. One potential consequence of such common mechanisms would be that improvements in one domain—the eye—should transfer to the other—the hand. Yet, the current study showed that training eye movements alone was not sufficient to improve hand movements, revealing no transfer from eye to hand (**Fig. 3**). This result was obtained regardless of the type of eye movement training employed (i.e., with or without feedback). Transfer of learning across modalities might only be possible if task requirements are strongly aligned and rely on the same processing mechanisms. Szpiro et al. (2014) observed transfer from perception to pursuit in a motion discrimination task that required perceptual estimation of the target's motion direction. There is considerable overlap in the neural mechanisms underlying motion perception and smooth pursuit (Lisberger, 2010; Osborne et al., 2005; Spering & Montagnini, 2011), facilitating transfer from motion perception to motion tracking. Even though there is evidence for interdependency between the neural control of eye and hand movements, particularly within posterior parietal cortex (Snyder, Batista, & Andersen, 1997; Buneo &

Andersen; 2006; Cui & Andersen, 2007; Battaglia-Mayer, Ferrari-Toniolo, & Visco-Comandini, 2015), both types of movement are ultimately controlled by effector-specific networks. Moreover, there is little research on the neural mechanisms underlying pursuit-hand coordination, and the extent of overlap between the cortical architecture underlying each type of movement is unclear. Finally, our current task was more complex and required not only processing of sensory motion information, but also trajectory prediction, based on past experience. Lack of transfer could indicate that the process of integrating sensory with experience-based information might differ for pursuit and hand movements.

In sum, our finding of lack of transfer from eye to hand is congruent with much of the perceptual learning literature indicating specificity of learning (Fahle, 2005). It emphasizes the importance of designing training tasks whose requirements mimic real-world requirements across diverse areas of application (e.g., a particular type of move in sports, or clinical rehabilitation).

Eye movements improve most when training involves a sensorimotor decision

We found that training smooth pursuit eye movements alone was also not sufficient to improve eye movement accuracy. Our training group 1 merely viewed the target briefly and tracked it with their eyes; these observers never saw the target end position in the hit zone. As a result, neither eye nor hand movements improved as compared to the control group. This finding is consistent with literature on eye movement training, showing only marginal improvements in pursuit velocity gain after training (Guo & Raymond, 2010; Szpiro et al., 2014). Yet, some studies have reported beneficial effects of smooth pursuit training. Experimentally naïve monkeys showed higher pursuit velocity and fewer catch-up saccades after many rigorous training sessions (Bourrelly, Quinet, Cavanagh, & Goffart, 2016). Moreover, engaging in contralesional pursuit improved functional recovery in human patients with visual neglect (Kerkhoff et al., 2013; Kerkhoff et al., 2014). These studies differ from ours in many aspects—study subjects, type of stimulus and task, and probably most importantly, duration and intensity of training. It is possible that prolonged pursuit training over many weeks could have increased pursuit performance in our study. Congruent with this assumption, group 1 was the only group displaying a small trend towards further improvement when tested again one week after training had been completed (**Fig. 3d; 5d**).

Interestingly, when pursuit training was paired with the instruction to make an eye movement toward the assumed target position in the hit zone (group 2), eye movements improved considerably. This improvement could be due to a combination of factors, including the preparation and execution of a goal-directed saccadic eye movement (**Fig. 6**), the predictive sensorimotor decision underlying this saccade, or motivational aspects related to external performance feedback. Feedback did not differentially affect eye movement performance in groups where training involved the hand (**Fig. 5c**). It is therefore unlikely that the difference between the two eye-training groups was entirely driven by feedback. Instead, differences in eye movement behavior, most notably an early goal-directed saccade and overall shorter and more accurate tracking in group 2, could underlie the finding that training in group 2 was more effective. Making an interceptive saccade comprises a different behavioral goal than just tracking a moving target without any task related to its trajectory; it requires prediction based on experience from previous trials (location of feedback) and integration with current sensory information (initial launch trajectory). Eye movements generally reflect the requirements of visual-motor tasks such as reaching, grasping, or walking (Hayhoe & Ballard, 2005; Hayhoe, 2017). Along the same lines, the behavioral goal of intercepting the target with the eyes might determine the need for accurate trajectory prediction, which in turn can only be achieved with accurate pursuit (Spering et al., 2011).

Finally, we acknowledge that we attributed beneficial effects of training that engaged the hand to the fact that the hand performed a goal-directed movement, involving a sensorimotor decision. Alternatively, improvements might be possible just based on engaging the hand in any kind of movement. This possibility could be tested by including a control group that engages in an independent pointing or hand movement task, not training the observer in the primary task.

External performance feedback did not modulate training

Providing external performance feedback generally boosts effects of training in visual (Deveau et al., 2014) and motor tasks (Swinnen, 1996; Sigrist et al., 2013). Gray (2009) compared swing accuracy in a baseball batting simulator when giving visual, auditory, or tactile feedback, respectively, to a no-feedback condition. Swings were more accurate when feedback was given, and visual feedback produced the greatest accuracy. However, feedback might not be critical for learning to occur: beneficial effects of training have been repeatedly reported in the absence of feedback (Herzog & Fahle, 1997; Liu, Lu, & Dosher, 2010; Szpiro et al., 2014). In our study, feedback significantly altered performance on training days (**Fig. 3b; 5b**) but did not significantly modulate training outcome.

It is possible that effects of external performance feedback were attenuated by the existence of both visual as well as internally generated feedback. In versions of the task that involved hand movements, observers were always able to see their own hand and thus received a strong visual feedback signal. Moreover, with every movement we make, the brain sends a copy of the movement command—an efference copy or corollary discharge—back to sensory brain areas, which then integrate these feedback signals with sensory input (Bridgeman, 1995; Crapse

& Sommer, 2008; Sommer & Wurtz, 2008). Another source of internal feedback information comes from proprioceptive information signaling the position of the eye in the orbit, or the arm in space (Ren et al., 2006; Vercher, Gauthier, Cole, & Blouin, 1997). Visual and internally generated feedback information might have boosted training across all training groups in our study, rendering external performance feedback less important than in studies involving perceptual judgments, where no visual or internally-generated feedback is automatically available.

Seeing the hand while it moves, especially close to the time of interception, provides important information needed to correct movements online (de la Malla, López-Moliner, & Brenner, 2012) and boosts spatial accuracy (de la Malla & López-Moliner, 2012). Further evidence for beneficial effects of visual and internally-generated feedback on motor task performance comes from the neglect literature. Patients with hemispatial neglect (e.g., following stroke) show severe biases in processing visual information presented in their contralesional hemifield. Yet, they can be surprisingly accurate when performing motor tasks, such as goal-directed hand movements, in their blind hemifield (Harvey, Jackson, Newport, Krämer, Morris, & Dow, 2001; Himmelbach & Karnath, 2003; Harvey & Rossit, 2012). This finding has been attributed in part to the availability of visual information (seeing the arm move in space); it could also be due to internally-generated feedback (efference copy and proprioceptive feedback).

Conclusion

Our results highlight the importance of a naturalistic task design to successfully train observers' sensorimotor performance. Learning is optimal when the training task involves a sensorimotor decision, here: an active interception of the target either by eye or hand movement. We found no direct transfer of training from eye to hand, indicating that cross-modality transfer likely requires co-activation of the neural networks underlying trained effectors. Our results also revealed only little influence of external performance feedback on training outcome, indicating that internally generated feedback during learning may be sufficient to boost eye and hand movement accuracy and precision.

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References

Bahill, A. T., & LaRitz, T. (1984). Why can't batters keep their eyes on the ball? *American Scientist, 72,* 249–253.

Ballard, D. H., Hayhoe, M. M., Li, F., & Whitehead, S. D. (1992). Hand-eye coordination during sequential tasks. *Philosophical Transactions of the Royal Society B*, *337*, 331–338.

Battaglia-Mayer, A., Ferrari-Toniolo, S., & Visco-Comandini, F. (2015). Timing and communication of parietal cortex for visuomotor control. *Current Opinion in Neurobiology*, *33*, 103–109.

Bekkering, H., & Sailer, U. (2002). Commentary: coordination of eye and hand in time and space. *Progress in Brain Research, 140*, 365–373.

Bennett, S., Orban de Xivry, J. J., Barnes, G. R., & Lefèvre, P. (2007). Target acceleration can be extracted and represented within the predictive drive to ocular pursuit. *Journal of Neurophysiology, 98*, 1405-1414.

Bennett, S. J., Baures, R., Hecht, H., & Benguigui, N. (2010). Eye movements influence estimation of time-to-contact in prediction motion. *Experimental Brain Research*, *206*, 399–407.

Bourrelly, C., Quinet, J., Cavanagh, P., & Goffart, L. (2016). Learning the trajectory of a moving visual target and evolution of its tracking in the monkey. *Journal of Neurophysiology*, *116*, 2739–2751.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*, 433-436.

Brenner, E., & Smeets, J. B. J. (2011). Continuous visual control of interception. *Human Movement Science*, *30*, 475–494.

Bridgeman, B. (1995). A review of the role of efference copy in sensory and oculomotor control systems. *Annals of Biomedical Engineering*, *23*, 409–422.

Buneo, C. A., & Andersen, R. A. (2006). The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia*, *44*, 2594–2606.

Cesqui, B., Mezzetti, M., Lacquaniti, F., & d'Avella, A. (2015). Gaze behavior in one-handed catching and its relation with interceptive performance: What the eyes can't tell. *PLoS One*, *10*(3), e0119445.

Crapse, T. B., & Sommer, M. A. (2008). Corollary discharge across the animal kingdom. *Nature Reviews Neuroscience*, *9*, 587–600.

Cui, H., & Andersen, R. A. (2007). Posterior parietal cortex encodes autonomously selected motor plans. *Neuron, 56*, 552–559.

de la Malla, C., & López-Moliner, J. (2012). How timely can our hand movements be? *Human Movement Science, 31*, 1103–1117.

de la Malla, C., López-Moliner, J., & Brenner, E. (2012). Seeing the last part of a hitting movement is enough to adapt to a temporal delay. *Journal of Vision, 12(10)*, 4.

de la Malla, C., Smeets, J. B. J., & Brenner, E. (2017). Potential systematic interception errors are avoided when tracking the target with one's eyes. *Scientific Reports*, *7*(1), 10793.

Dempsey-Jones, H., Harrar, V., Oliver, J., Johansen-Berg, H., Spence, C., & Makin, T. R. (2016). Transfer of tactile perceptual learning to untrained neighboring fingers reflects natural use relationships. *Journal of Neurophysiology, 115*, 1088–1097.

Deveau, J., Ozer, D. J., & Seitz, A. R. (2014). Improved vision and on-field performance in baseball through perceptual learning. *Current Biology*, *24*, R146–R147.

Diaz, G., Cooper, J., Rothkopf, C., & Hayhoe, M. (2013). Saccades to future ball locations reveal memory-based prediction in a virtual-reality interception task. *Journal of Vision, 13(1)*, 20, 1–14.

Dunnett, C. W. (1955). A multiple comparison procedure for comparing several treatments with a control. *Journal of the American Statistical Association, 50*, 1096-1121.

Fahle, M. (2005). Perceptual learning: Specificity versus generalization. *Current Opinion in Neurobiology*, *15*, 154–160.

Fahle, M., & Edelman, S. (1993). Long-term learning in vernier acuity: Effects of stimulus orientation, range and of feedback. *Vision Research*, *33*, 397–412.

Fahle, M., & Poggio, T. (Eds.). (2002). *Perceptual learning*. Cambridge, MA: MIT Press.

Faubert, J. (2013). Professional athletes have extraordinary skills for rapidly learning complex and neutral dynamic visual scenes. *Scientific Reports, 3*(1154), 1–3.

Fooken, J., Lalonde, K. M., & Spering, M. (2016). When hand movements improve eye movement performance. *Journal of Vision, 16(12)*, 374.

Fooken, J., Yeo, S.-H., Pai, D. K., & Spering, M. (2016). Eye movement accuracy determines natural interception strategies. *Journal of Vision*, *16*(14), 1–15.

Gray, R. (2009). How do batters use visual, auditory, and tactile information about the success of a baseball swing? *Research Quarterly for Exercise and Sport*, *80*, 491–501.

Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature*, *423*, 534–537.

Green, C. S., & Bavelier, D. (2007). Action-video-game experience alters the spatial resolution of vision. *Psychological Science*, *18*, 88–94.

Green, C. S., & Bavelier, D. (2012). Learning, attentional control, and action video games. *Current Biology*, *22*, R197–R206.

Gribble, P. L., Everling, S., Ford, K., & Mattar, A. (2002). Hand-eye coordination for rapid pointing movements. *Experimental Brain Research*, *145*, 372–382.

Guo, C. C., & Raymond, J. L. (2010). Motor learning reduces eye movement variability through reweighting of sensory inputs. *Journal of Neuroscience*, *30*, 16241–16248.

Harvey, M., Jackson, S. R., Newport, R., Krämer, T., Morris, D. L., & Dow, L. (2001). Is grasping impaired in hemispatial neglect? *Behavioural Neurology, 13*, 17–28.

Harvey, M., & Rossit, S. (2012). Visuospatial neglect in action. *Neuropsychologia, 50*, 1018–1028.

Hayhoe, M. M., & Ballard, D. (2005). Eye movements in natural behavior. *Trends in Cognitive Sciences*, *9*, 188–194.

Hayhoe, M. M. (2017). Vision and action. *Annual Review in Vision Science, 3*, 1–25.

Herzog, M. H., & Fahlet, M. (1997). The role of feedback in learning a vernier discrimination task. *Vision Research*, *37*, 2133–2141.

Herzog, M. H., & Fahle, M. (1999). Effects of biased feedback on learning and deciding in a vernier discrimination task. *Vision Research*, *39*, 4232–4243.

Himmelbach, M., & Karnath, H. O. (2003). Goal-directed hand movements are not affected by the biased space representation in spatial neglect. *Journal of Cognitive Neuroscience, 15*, 972–980.

Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye-hand coordination in object manipulation. *Journal of Neuroscience*, *21*, 6917–6932.

Kreyenmeier, P., Fooken, J., & Spering, M. (2017). Context effects on smooth pursuit and manual interception of a disappearing target. *Journal of Neurophysiology*, *118*, 404–415.

Land, M. F., & McLeod, P. (2000). From eye movements to actions: How batsmen hit the ball. *Nature Neuroscience*, *3*(12), 1340–1345.

Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in Retinal and Eye Research*, *25*, 296–324.

Land, M., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception*, *28*, 1311–1328.

Leclercq, G., Blohm, G., & Lefèvre, P. (2013). Accounting for direction and speed of eye motion in planning visually guided manual tracking. *Journal of Neurophysiology, 110*, 1945–1957.

Levi, D. M., & Li, R. W. (2009). Perceptual learning as a potential treatment for amblyopia: A mini-review. *Vision Reserach*, *49*, 2535–2549.

Li, L., Chen, R., & Chen, J. (2016). Playing action video games improves visuomotor control. *Psychological Science*, *27*, 1092–1108.

Lisberger, S. G. (2010). Visual guidance of smooth-pursuit eye movements: sensation, action, and what happens in between. *Neuron, 66*, 477–491.

Liu, J., Lu, Z.-L., & Dosher, B. A. (2010b). Augmented Hebbian reweighting: Interactions between feedback and training accuracy in perceptual learning. *Journal of Vision*, *10*, 1–14.

López-Moliner, J., & Brenner, E. (2016). Flexible timing of eye movements when catching a ball. *Journal of Vision*, *16*(5), 1–11.

Mann, D. L., Spratford, W., & Abernethy, B. (2013). The head tracks and gaze predicts: how the world's best batters hit a ball. *PLoS ONE, 8(3)*, e58289.

Neggers, S. F. W., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology*, *83*, 639–651.

Osborne, L. C., Lisberger, S. G. & Bialek, W. (2005). A sensory source for motor variation. *Nature, 437*, 412–416.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision, 10*, 437–442.

Polat, U., & Sagi, D. (1994). Spatial interactions in human vision: From near to far experience-dependent cascades of connections. *Proceedings of the National Academy of Sciences*, *91*, 1206–1209.

Porat, Y., & Zohary, E. (2016). Practice improves peri-saccadic shape judgment but does not diminish target mislocalization. *Proceedings of the National Academy of Sciences, 113*, 7327-7336.

Ren, L., Khan, Z., Blohm, G., Henriques, D. Y. P., Sergio, L. E., & Crawford, J. D. (2006). Proprioceptive guidance of saccades in eye-hand coordination. *Journal of Neurophysiology*, *96*, 1464–1477.

Sailer, U., Flanagan, J. R., & Johansson, R. S. (2005). Eye-hand coordination during learning of a novel visuomotor task. *Journal of Neuroscience*, *25*, 8833– 8842.

Salmoni, A. W., Schmidt, R. A., & Walter, C. B. (1984). Knowledge of results and motor learning: A review and critical reappraisal. *Psychological Bulletin*, *95*, 355–386.

Sigrist, R., Rauter, G., Riener, R., & Wolf, P. (2013). Augmented visual, auditory, haptic, and multimodal feedback in motor learning: A review. *Psychonomic Bulletin & Review*, *20*, 21–53.

Smeets, J. B., Hayhoe, M. M., & Ballard, D. H. (1996). Goal-directed arm movements change eye-head coordination. *Experimental Brain Research*, *109*, 434–440.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature, 386*, 167–170.

Sommer, M. A., & Wurtz, R. H. (2008). Visual perception and corollary discharge. *Perception*, *37*, 408–418.

Spering, M., & Montagnini, A. (2011). Do we track what we see? Common versus independent processing for motion perception and smooth pursuit eye movements: A review. *Vision Research*, 51, 836–852.

Spering, M., Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Keep your eyes on the ball: smooth pursuit eye movements enhance prediction of visual motion. *Journal of Neurophysiology*, *105*, 1756–1767.

Swinnen, S. P. (1996). Information feedback for motor skill learning: a review. In N. Zelaznik (Ed.), *Advances in motor learning and control* (pp. 37-66). Champaign, IL: Human Kinetics.

Swinnen, S. P., Lee, T. D., Verschueren, S., Serrien, D. J., & Bogaerds, H. (1997). Interlimb coordination: learning and transfer under different feedback conditions. *Human Movement Science*, *16*, 749–785.

Szpiro, S. F., Spering, M., & Carrasco, M. (2014). Perceptual learning modifies untrained pursuit eye movements. *Journal of Vision*, *14*(8), 1–13.

Tanaka, K., & Watanabe, K. (2017). Explicit instruction of rules interferes with visuomotor skill transfer. *Experimental Brain Research*, *235*, 1689–1700.

Uchida, Y., Kudoh, D., Higuchi, T., Honda, M., & Kanosue, A. K. (2013). Dynamic visual acuity in baseball players is due to superior tracking abilities. *Medicine and Science in Sports and Exercise*, *45*, 319–325.

van Donkelaar, P., Lee, R. G., & Gellman, R. S. (1994). The contribution of retinal and extraretinal signals to manual tracking movements. *Experimental Brain Research*, *99*, 155–163.

Vazquez, Y., Federici, L., & Pesaran, B. (2017). Multiple spatial representations interact to increase reach accuracy when coordinating a saccade with a reach. *Journal of Neurophysiology, 118*, 2328–2343.

Vercher, J. L., Gauthier, G. M., Cole, J., & Blouin, J. (1997). Role of arm proprioception in calibrating the arm-eye temporal coordination. *Neuroscience Letters*, *237*, 109-112.

Vickers, J. N. (2016). Origins and current issues in Quiet Eye research. *Current Issues in Sport Science*, *1*(1), 1–11.

Werner, S., & Bock, O. (2007). Effects of variable practice and declarative knowledge on sensorimotor adaptation to rotated visual feedback. *Experimental Brain Research*, *178*, 554–559.

Wolpert, D. M., Diedrichsen, J., & Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nature Reviews Neuroscience*, *12,* 739–751.

Xiao, L.-Q., Zhang, J.-Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology*, *18*, 1922–1926.

Figure captions

Figure 1. Experimental procedure and design. Stimuli moved at one of three different speeds, resulting in three trajectory types (a), and were presented for either 100, 200, or 300 ms. An example trial sequence from the pretest track-intercept task is presented in (b). Each trial started with fixation in the "tracking zone", followed by stimulus motion for 100-300 ms. Observers were instructed to track the target with their eyes even after it disappeared, and to intercept it anywhere within the "hit zone" with their index finger. Performance feedback was given after each trial. On training days (c), observers were instructed to either track the target with their eyes (groups 1 & 2), or to intercept with their finger (groups 3 & 4). Only groups 2 and 4 received performance feedback during training; group 5 was not trained and served as the control group.

Figure 2. Schematic predictions of training effects. The graphs in (a) illustrate expected improvements after training as compared to the control group within each modality (Hypothesis 1a, H_0 not shown) and potential boost across each modality (Hypothesis 1b, transparent bars). Graphs in (b) illustrate the expected effect of feedback on performance (Hypothesis 2, transparent bars). If feedback had no effect on eye and hand movement accuracy results would be equivalent to panel (a).

Figure 3. 2D interception positions of two representative observers in group 5 (no training; top row) and two observers in group 4 (eye-hand training with feedback; bottom row); each data point denotes interception position in one trial in the pre-test (closed symbols) or post-test (open symbols). Target speeds are denoted by line color and presentation durations by symbol type.

Figure 4. Training effects on manual interception accuracy. (a) Interception error (in degrees) during pre-test vs. post-test. Each data point is the mean 2D interception error for one observer across all trials; larger data points with 2D error bars are group means. Data points falling above the unity line indicate higher error during the post-test, data points below the unity line denote higher error during the pre-test. (b) Interception accuracy increase (deg) in comparison to the pre-test, with error during pre-test set to zero, for all testing and training days. (c) Percentage accuracy increase (error decrease) in post-test relative to pre-test. Asterisks denote significant results of Dunnett's t-test, * $p < .05$. (d) Absolute interception error averaged across observers that came for the week follow up for post- (darker) compared to week-test (lighter). Asterisks denote significant results of pairwise t-test, * $p < .05$, *** $p < .001$. Error bars in all panels denote standard errors of the mean.

Figure 5. Mean interception error in response to three different speed conditions across time; (a) Group 5 (no training), (b) group 4 (eye-hand training with feedback). Values for pre- and post-test are averaged within bins of 9 trials. Values for training days are averaged across session (n = 486 trials). Filled symbols denote group mean, open symbols are means per subject.

Figure 6. 2D interception variance (precision) in pre-test (outer ellipse) as compared to post-test (inner ellipse) for all groups averaged across conditions and observers.

Figure 7. Training effects on eye interception accuracy. (a) Interception error (in degrees) during pre-test vs. post-test. Each data point is the mean 2D interception error for one observer across all trials; larger data points with 2D error bars are group means. Data points falling above the

unity line indicate higher error during the post-test, data points below the unity line denote higher error during the pre-test. (b) Interception accuracy increase (deg) relative to the pre-test, with error during pre-test set to zero, for all testing and training days. (c) Percentage accuracy increase (error decrease) in post-test relative to pre-test.

Figure 8. Mean eye velocity traces as a function of time relative to target motion onset across all observers (*n* = 10 per group; one panel per group). Saccades were replaced by linear interpolation. Line style denotes testing or training day.

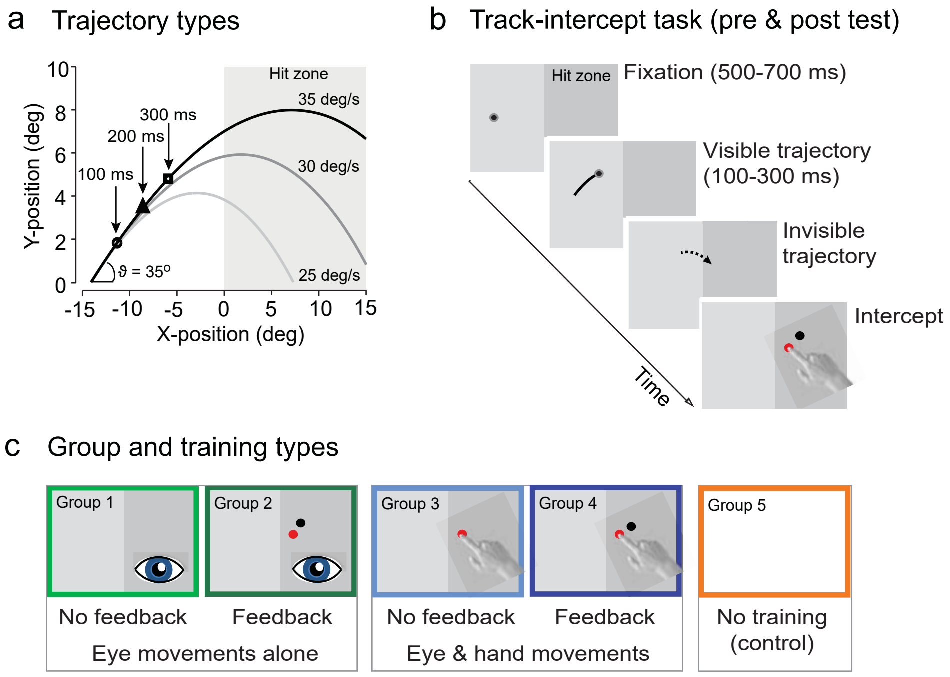
Figure 9. Training effects on eye movement accuracy. (a) Relative eye velocity during pre-test vs. post-test. Each data point is the mean relative velocity for one observer across all trials; larger data points are group means. Data points falling above the unity line indicate higher relative velocity during the post-test, data points below the diagonal denote higher relative velocity during the pre-test. (b) Relative velocity change in comparison to the pre-test, with relative velocity during pre-test set to zero, for all testing and training days. (c) Percentage velocity increase in post-test relative to pre-test. Asterisks denote significant results of Dunnett's t-test, * $p < .05$, ** $p < .01$. (d) Relative velocity averaged across observers that came for the week follow up for post- (darker) compared to week-test (lighter). Error bars in all panels denote standard errors.

Figure 10. (a) Horizontal and vertical eye position for a representative observer in group 1 (eye training no feedback) for a single trial during a training day. Black line denotes average target path shown until time of interception, the vertical grey line denotes point of target disappearance

at 200 ms. (b) Eye position of a representative observer in group 2 (eye training with feedback) in two trials in which the target disappeared after 200 ms. In both panels the target entered the hit zone at 1,000 ms after target onset. (c) Horizontal and vertical eye position as a function of time for one representative trial from the same observer as in (a). (d) Horizontal and vertical eye position for the same observer as in (b).

Table 1. Training protocols for five groups. Training on days 2-4 could include eye movements only (eye), or combined eye and hand movements (eye-hand); it either involved external performance feedback (FB) or not. Pre- and post-test were identical across groups. Number of observers during follow-up testing varied by group.

Group (*n* = 10 each)	Mean age (SD)	Gender (*n* female)	Pre-test (day 1)	Training (days 2-4)			Post-test (day 5)	Follow-up *n* (day 12)
				eye	hand	FB		
(1) eye no FB	24.5 (3.8)	6	✓	✓			✓	9
(2) eye FB	25.6 (4.2)	6	✓	✓		✓	✓	9
(3) eye-hand no FB	23.9 (3.6)	6	✓	✓	✓		✓	10
(4) eye-hand FB	24 (2.3)	6	✓	✓	✓	✓	✓	5
(5) no training	23 (3.3)	5	✓				✓	8

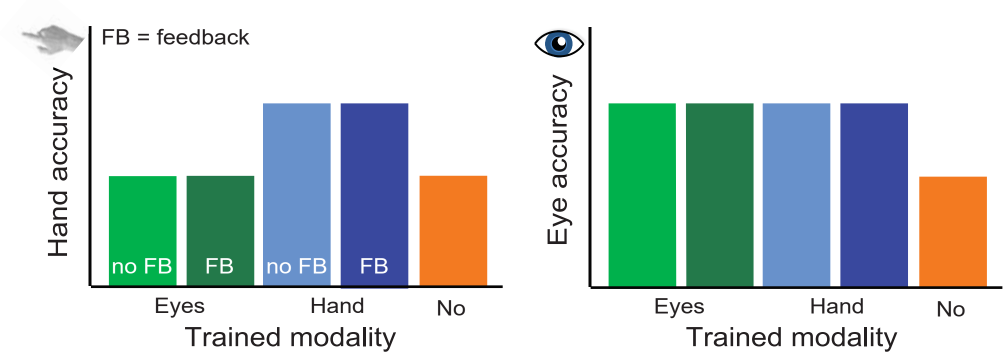

a
Trajectory types
Hit zone
35 deg/s
30 deg/s
25 deg/s
300 ms
200 ms
100 ms
ϑ = 35°
Y-position (deg)
0
2
4
6
8
10
-15
-10
-5
0
5
10
15
X-position (deg)
b
Track-intercept task (pre & post test)
Hit zone
Fixation (500-700 ms)
Visible trajectory (100-300 ms)
Invisible trajectory
Intercept
Time
c
Group and training types
Group 1
Group 2
Group 3
Group 4
Group 5
No feedback
Feedback
Eye movements alone
No feedback
Feedback
Eye & hand movements
No training (control)

a

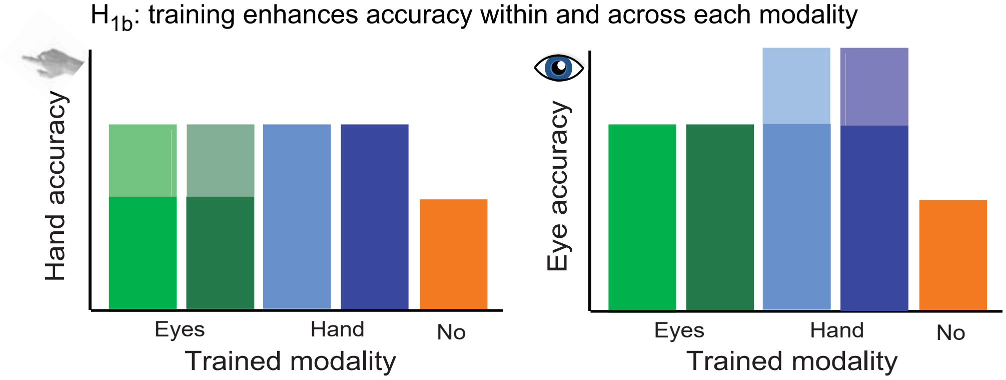
Hypothesis 1: training improves movement accuracy

H_0: training does not improve movement accuracy compared to control group

H_{1a}: training increases movement accuracy within each modality



H_{1b}: training enhances accuracy within and across each modality

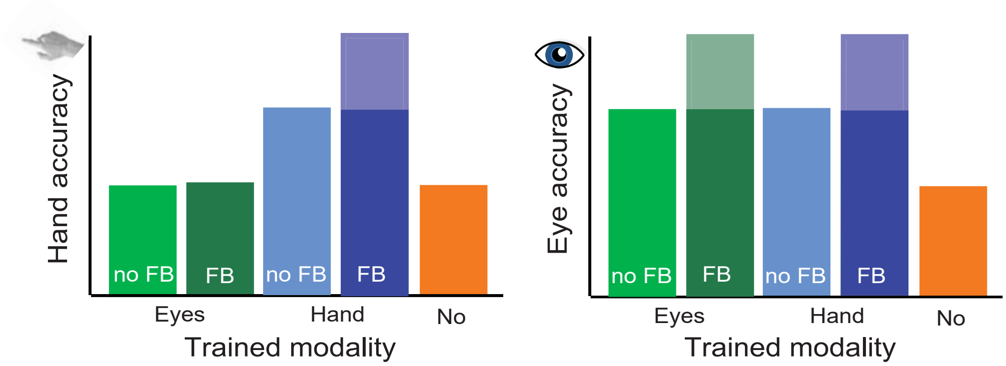


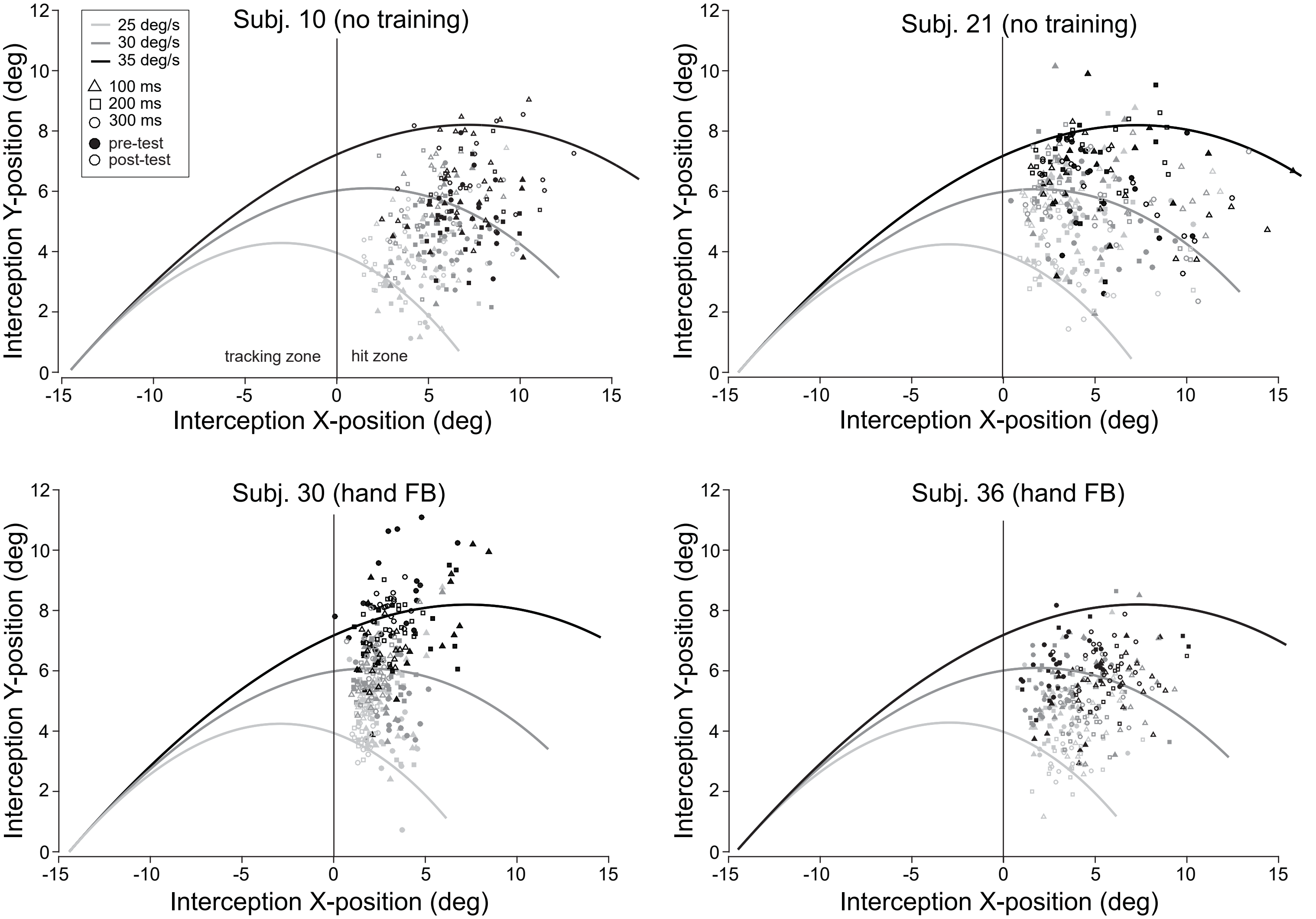
b

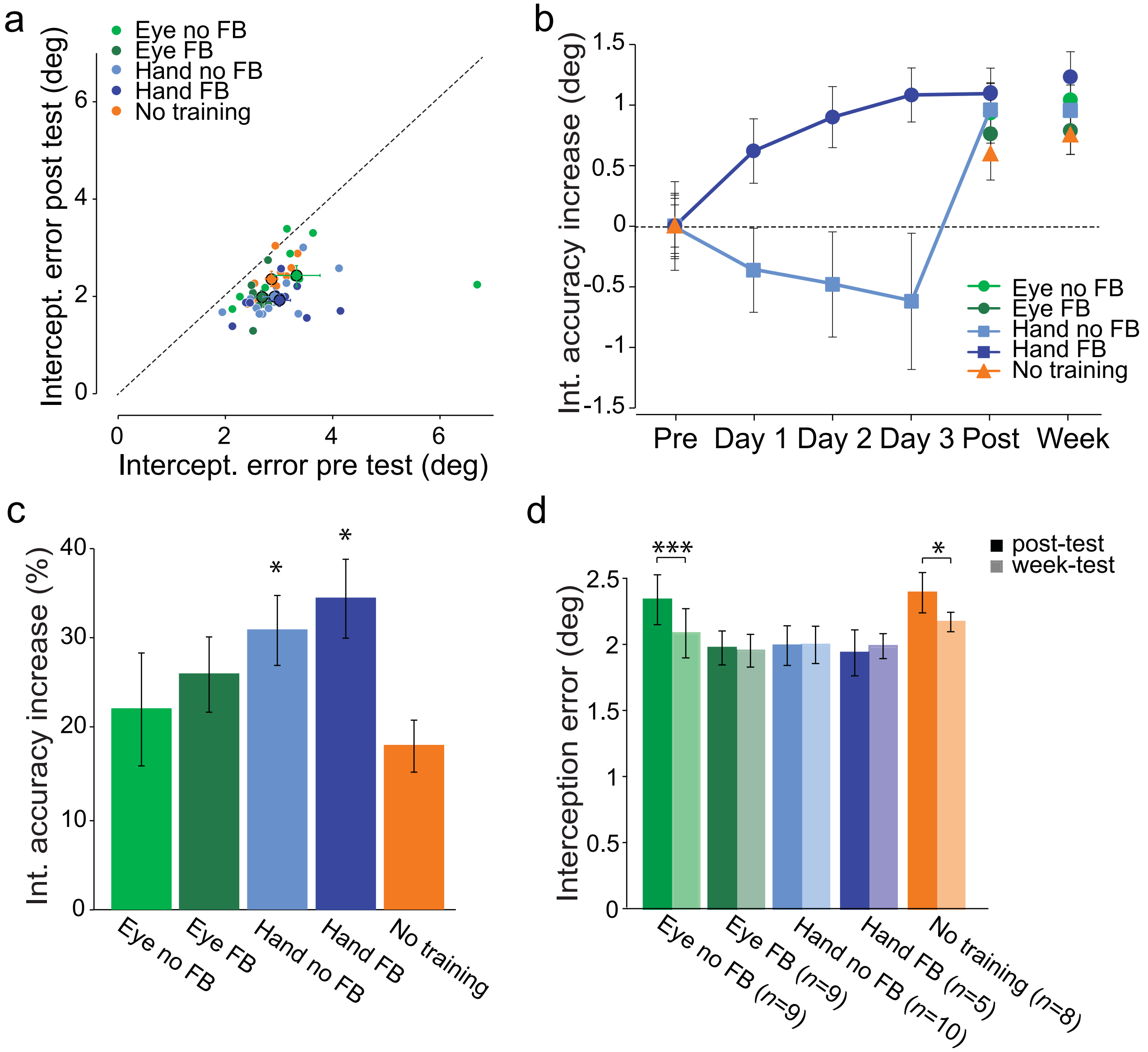
Hypothesis 2: feedback enhances training effects

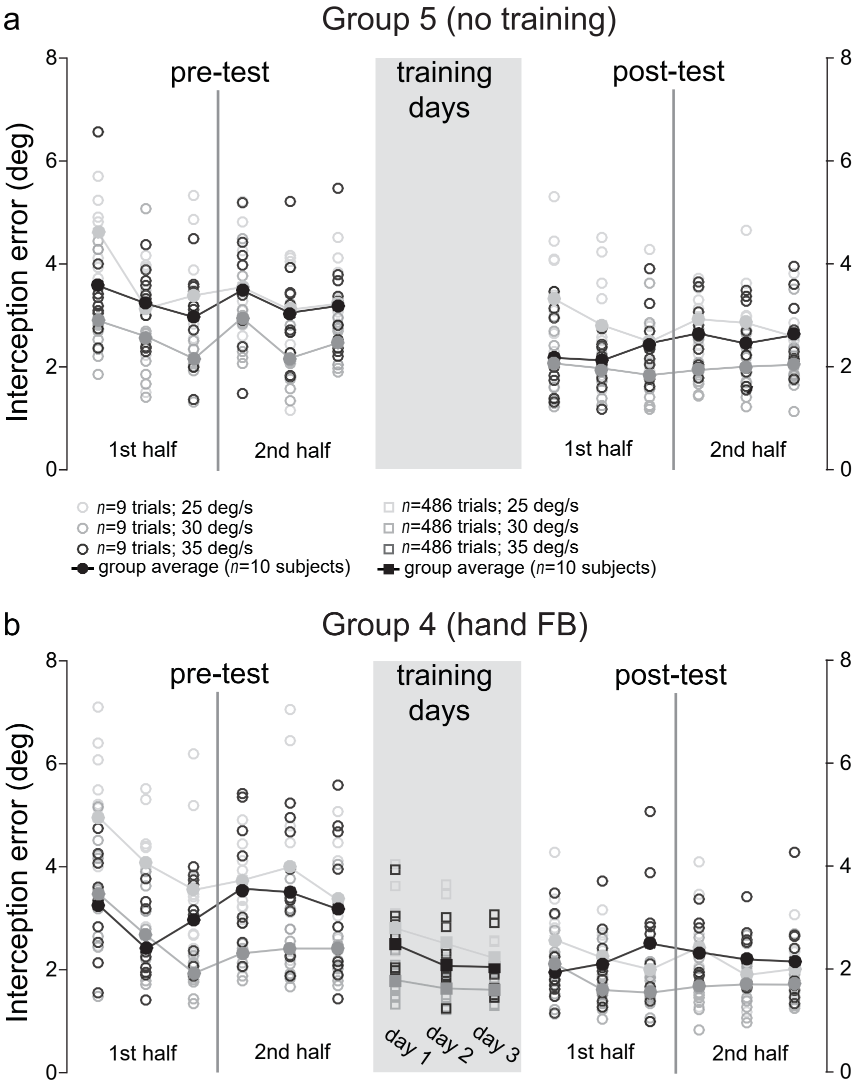
H_0: feedback during training has no differential effect on movement accuracy

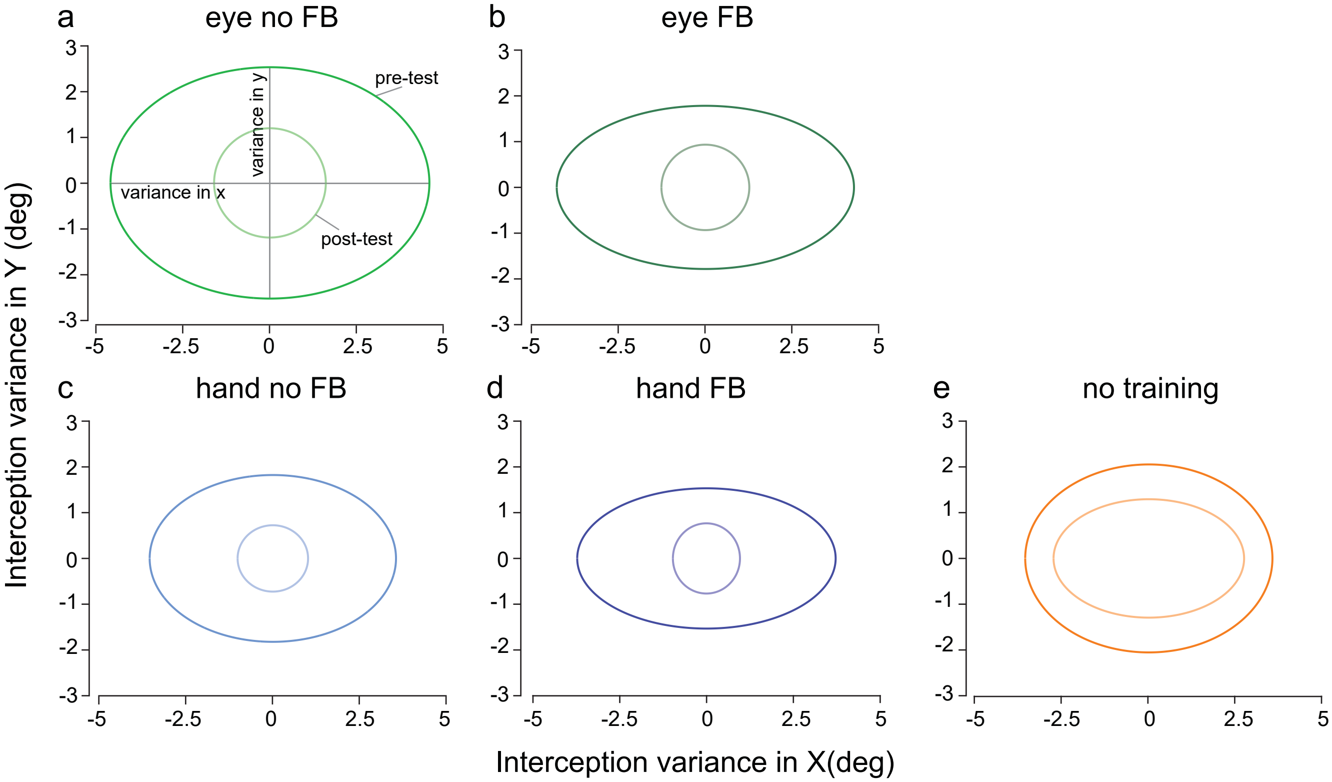
H_1: feedback enhances training effects within each movement modality



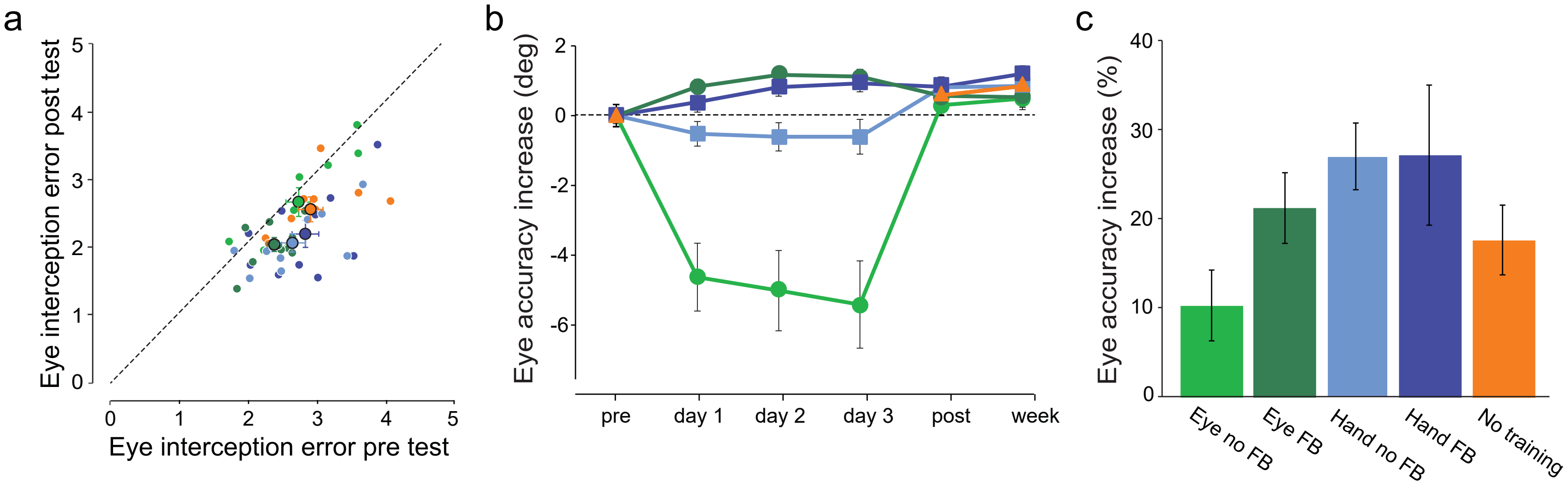

Subj. 10 (no training)
Subj. 21 (no training)
Subj. 30 (hand FB)
Subj. 36 (hand FB)
25 deg/s
30 deg/s
35 deg/s
△ 100 ms
□ 200 ms
○ 300 ms
● pre-test
○ post-test
tracking zone
hit zone
Interception Y-position (deg)
Interception X-position (deg)
0
2
4
6
8
10
12
-15
-10
-5
0
5
10
15

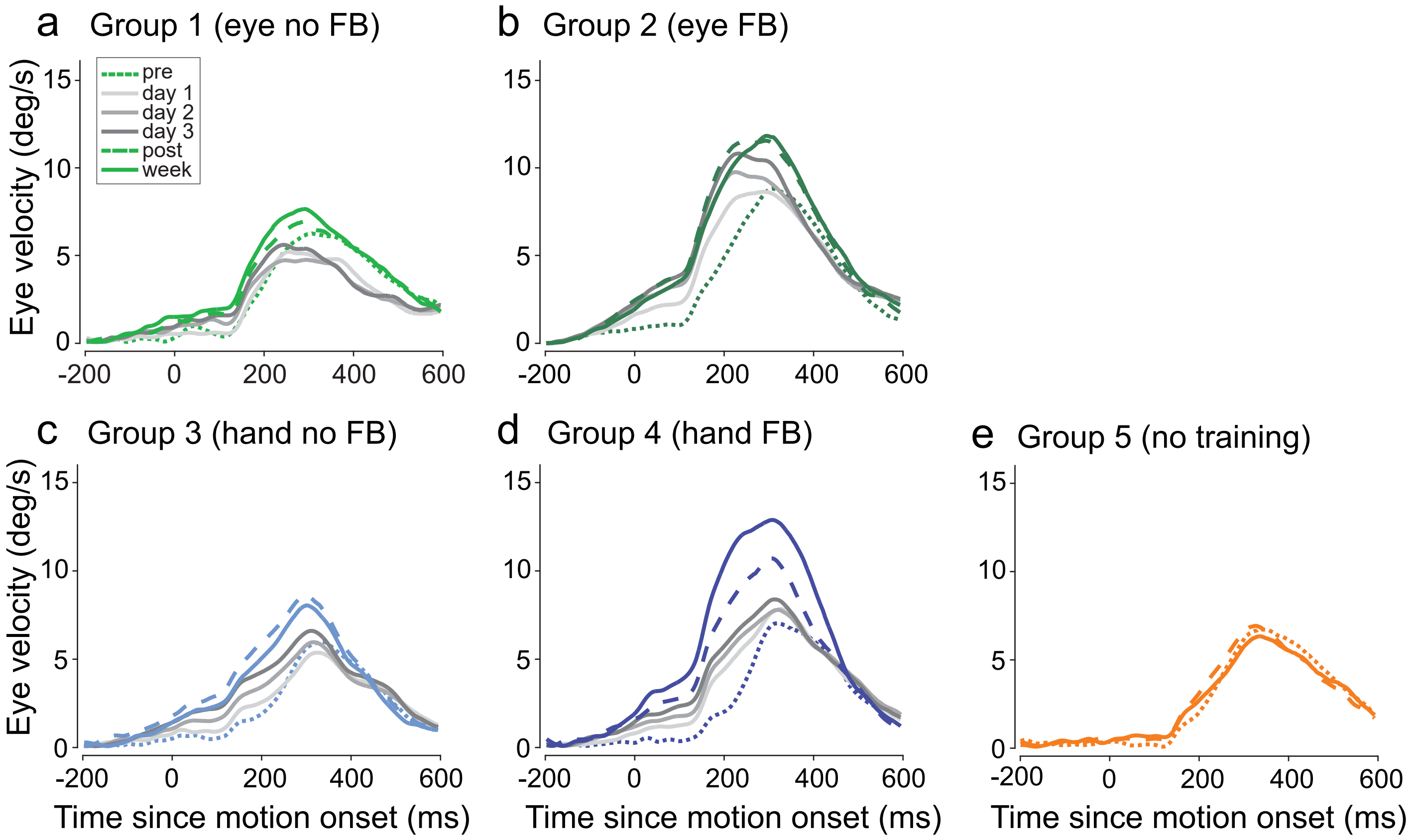

a
Eye no FB
Eye FB
Hand no FB
Hand FB
No training
Intercept. error post test (deg)
0
2
4
6
Intercept. error pre test (deg)
b
Int. accuracy increase (deg)
1.5
1
0.5
0
-0.5
-1
-1.5
Pre
Day 1
Day 2
Day 3
Post
Week
Eye no FB
Eye FB
Hand no FB
Hand FB
No training
c
Int. accuracy increase (%)
40
30
20
10
0
*
*
Eye no FB
Eye FB
Hand no FB
Hand FB
No training
d
post-test
week-test
Interception error (deg)
2.5
2
1.5
1
0.5
0
***
*
Eye no FB (n=9)
Eye FB (n=9)
Hand no FB (n=10)
Hand FB (n=5)
No training (n=8)

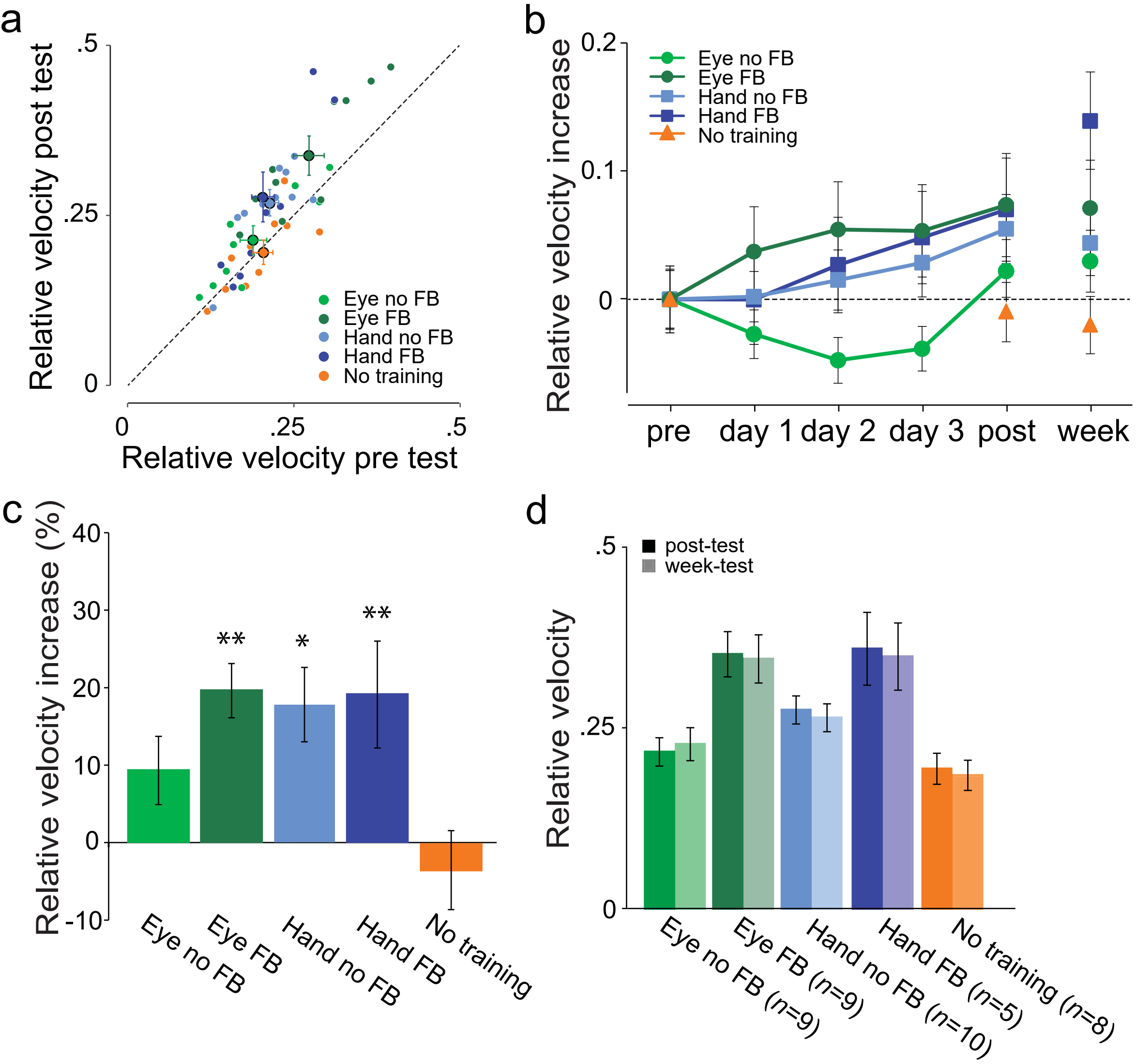

a
Group 5 (no training)
Interception error (deg)
0
2
4
6
8
pre-test
training days
post-test
1st half
2nd half
1st half
2nd half
○ n=9 trials; 25 deg/s
○ n=9 trials; 30 deg/s
○ n=9 trials; 35 deg/s
● group average (n=10 subjects)
□ n=486 trials; 25 deg/s
□ n=486 trials; 30 deg/s
□ n=486 trials; 35 deg/s
■ group average (n=10 subjects)
b
Group 4 (hand FB)
Interception error (deg)
0
2
4
6
8
pre-test
training days
post-test
1st half
2nd half
day 1
day 2
day 3
1st half
2nd half

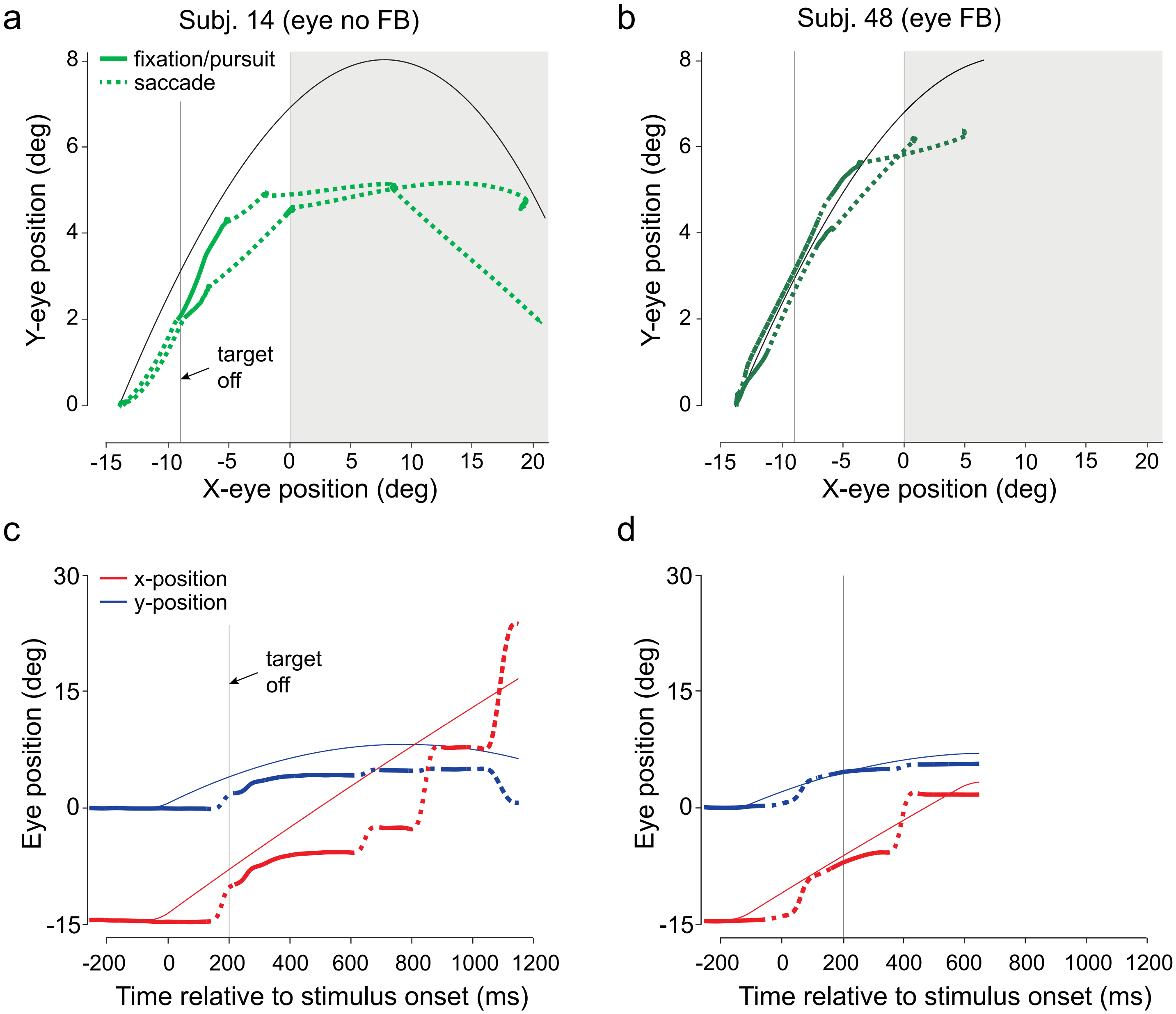


a
eye no FB
pre-test
variance in y
variance in x
post-test
b
eye FB
c
hand no FB
d
hand FB
e
no training
3
2
1
0
-1
-2
-3
-5
-2.5
0
2.5
5
Interception variance in Y (deg)
Interception variance in X(deg)


a
Eye interception error post test
Eye interception error pre test
0
1
2
3
4
5
b
Eye accuracy increase (deg)
2
0
-2
-4
-6
pre
day 1
day 2
day 3
post
week
c
Eye accuracy increase (%)
40
30
20
10
0
Eye no FB
Eye FB
Hand no FB
Hand FB
No training


a
Group 1 (eye no FB)
b
Group 2 (eye FB)
c
Group 3 (hand no FB)
d
Group 4 (hand FB)
e
Group 5 (no training)
pre
day 1
day 2
day 3
post
week
Eye velocity (deg/s)
0
5
10
15
-200
0
200
400
600
Time since motion onset (ms)


a
Relative velocity post test
Relative velocity pre test
.5
.25
0
0
.25
.5
Eye no FB
Eye FB
Hand no FB
Hand FB
No training
b
Relative velocity increase
0.2
0.1
0
Eye no FB
Eye FB
Hand no FB
Hand FB
No training
pre
day 1
day 2
day 3
post
week
c
Relative velocity increase (%)
40
30
20
10
0
-10
**
*
**
Eye no FB
Eye FB
Hand no FB
Hand FB
No training
d
Relative velocity
.5
.25
0
post-test
week-test
Eye no FB (n=9)
Eye FB (n=9)
Hand no FB (n=10)
Hand FB (n=5)
No training (n=8)


a
Subj. 14 (eye no FB)
fixation/pursuit
saccade
target off
Y-eye position (deg)
X-eye position (deg)
8
6
4
2
0
-15
-10
-5
0
5
10
15
20
b
Subj. 48 (eye FB)
c
x-position
y-position
target off
Eye position (deg)
30
15
0
-15
-200
0
200
400
600
800
1000
1200
Time relative to stimulus onset (ms)
d