



Microsaccades as a long-term oculomotor correlate in visual perceptual learning

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Abstract

Human perceptual learning, experience-induced gains in sensory discrimination, typically yields long-term performance improvements. Recent research revealed long-lasting transfer at the untrained location enabled by feature-based attention (FBA), reminiscent of its global effect (Hung & Carrasco, 2021). Visual Perceptual Learning (VPL) is typically studied while observers maintain fixation, but the role of fixational eye movements is unknown. Microsaccades – the largest of fixational eye movements – provide a continuous, online, physiological measure from the oculomotor system that reveals dynamic processing, which is unavailable from behavioral measures alone. We investigated whether and how microsaccades change after training in an orientation discrimination task. For human observers trained with or without FBA, microsaccade rates were significantly reduced during the response window in both trained and untrained locations and orientations. Critically, consistent with long-term training benefits, this microsaccade-rate reduction persisted over a year. Furthermore, microsaccades were biased toward the target location prior to stimulus onset and were more suppressed for incorrect than correct trials after observers' responses. These findings reveal that fixational eye movements and VPL are tightly coupled and that learning-induced microsaccade changes are long lasting. Thus, microsaccades reflect functional dynamics of the oculomotor system during information encoding, maintenance and readout, and may serve as a reliable long-term physiological correlate in VPL.

Keywords Perceptual learning · Eye movements · Visual attention

Introduction

Perceptual learning is the process by which humans refine the sensory systems through experience (Sagi, 2011). This learning process typically requires practice over several days, and performance improvements can last months or even years (Hung & Carrasco, 2021; Karni & Sagi, 1993; Yashar & Carrasco, 2016; Yashar et al., 2015). Perceptual learning provides important clues regarding how the neural circuitry changes through extensive training and has translational implications for improving perceptual skills in people seeking expertise (Deveau et al., 2014) or rehabilitation (Cavanaugh et al., 2019, 2022; Levi & Li, 2009; Roberts &

Carrasco, 2022; Yan et al., 2015). Most perceptual learning research has focused on visual perceptual learning (VPL). Here we investigate whether and how fixational eye movements – microsaccades – change with VPL.

Visual perceptual learning is typically specific to the trained stimulus location and orientation (Hung & Seitz, 2014; Karni & Sagi, 1991), and such specificity has been interpreted to indicate that VPL arises from neural plasticity in primary visual cortices (Furmanski et al., 2004; Schoups et al., 2001; Yotsumoto et al., 2008). Currently, however, VPL is considered to involve multiple brain systems, including those related to read-out, attention, feedback, decision, and oculomotor systems (Maniglia & Seitz, 2018). As our ability to discriminate visual information decreases with eccentricity, the extent to which VPL can improve fine stimulus discrimination has been assessed in peripheral locations (Donovan et al., 2020; Hung & Carrasco, 2021; Schoups et al., 2001). Thus, VPL studies are often carried out when observers maintain fixation.

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When we fixate, our eyes move incessantly and produce “fixational eye movements” which shift our gaze across the foveola ($\sim 1^\circ$ highest-acuity region at the center of gaze). Microsaccades, the largest and fastest fixational eye movements, typically occur one to two times per second with an amplitude $< 1^\circ$ (Martinez-Conde et al., 2013). Microsaccades maintain visibility by shifting the retinal image to overcome perceptual fading during sustained fixation (Martinez-Conde et al., 2006, 2013; McCamy et al., 2012), and improve fine spatial vision by properly relocating the gaze in high-acuity tasks (Ko et al., 2010; Rucci et al., 2007). As microsaccades provide a continuous, online physiological measure of the oculomotor system that can reveal dynamic processing, they are considered a window into a variety of cognitive functions, for example, spatial attention (Engbert & Kliegl, 2003; Xue et al., 2020; Yuval-Greenberg et al., 2014), temporal attention (Denison et al., 2019), temporal expectation (Abeles et al., 2020; Amit et al., 2019; Badde et al., 2020; Dankner et al., 2017) and working memory (van Ede et al., 2019; Willeke et al., 2019). However, microsaccades have not been systematically assessed with regard to VPL. It is unknown whether and how they change in classic VPL tasks in which fixation is maintained.

Here, we investigated whether and how microsaccades change when observers trained under a feature-based attention (FBA) or a control neutral condition in an orientation discrimination task. To assess long-term VPL effects, observers were re-tested 3–4 months and 1 year afterwards. We had found that training in a Neutral condition only yields learning at the trained location, whereas deploying FBA during training generalizes learning to other locations thus overcoming location specificity (Hung & Carrasco, 2021). Here, for all observers, regardless of whether they trained with FBA or in a neutral condition, training reduced microsaccade rates during the response window while observers were preparing for a key response, in both the trained and untrained locations and orientations. These changes likely reflect functional dynamics of the oculomotor system during maintenance and readout of information. Critically, consistent with our behavioral long-lasting effects (Hung & Carrasco, 2021), the VPL-induced microsaccade-rate reduction during the response window remained after 1 year. We also found that microsaccade directions were biased towards the target location prior to stimulus onset, an effect related to stimulus encoding. Additionally, microsaccade rates were higher for correct than incorrect trials while observers received feedback, i.e., during supervised learning. These results are the first to reveal that changes in fixational eye movements and VPL are tightly coupled and that learning-induced microsaccade changes are long lasting. Thus, microsaccades may serve as a reliable physiological marker in human VPL.

Materials and methods

Materials and Methods have been reported in Hung and Carrasco (2021).

Observers

Twenty (13 females; $M = 23.6 \pm 4.6$ years old) naïve human observers who had normal or corrected-to-normal vision participated in the experiment. The 20 observers were equally distributed into two groups – Neutral (five females; $M = 22.4 \pm 4.1$ years old) or Attention (eight females; $M = 24.8 \pm 5.0$ years old). Based on a power analysis using effect sizes from a recent VPL study (Donovan et al., 2020), we estimated the sample size as 9–10 per group to detect a similar learning effect with 80% power, given a 0.05 significance criterion. The experimental protocols were approved by the University Committee on Activities Involving Human Subjects of New York University, and all research was performed in accordance with relevant guidelines/regulations. Informed consent was obtained from all observers.

Apparatus

The stimuli were presented using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for MATLAB (The MathWorks, Natick, MA, USA) on an iMac computer with a 21-in. gamma-corrected Sony GDM-5402 CRT monitor with resolution of 1280×960 pixels and a refresh rate of 100 Hz. An infrared eye tracker system Eyelink 1000 (SR research, Kanata, Ontario, Canada) and a chin rest and head rest were used to ensure eye fixation at the center of the display throughout each trial in the experimental sessions. The viewing distance was 57 cm, and all experiments were performed with a gaze-contingent display in which the eye-tracker enabled new trials to start only once observers had fixated at the center (within a 2° radius fixation window). If an eye-movement outside of this window was detected at any point after the trial started, then that trial was aborted and added to the end of each block ($\sim 5\%$ of the trials).

Stimuli

In each trial, the stimulus was a single Gabor patch (Gaussian-windowed sinusoidal grating) subtending 2° of visual angle and presented at 5° eccentricity on a grey background. The Gabor had a spatial frequency of 4 cpd, standard deviation of 2λ , and Michelson contrast of 0.64. To assess five different difficulty levels, there were five offsets (2° , 4° , 6° , 8° , and 10°) that were either clockwise or counter-clockwise from reference angles. We used four

reference orientations, which indexed different features in this task, and at the beginning of each block two of the references (either reference combination 1 of 30°/120°, or combination 2 of 60°/150°) were presented simultaneously (Fig. 1B bottom). The neutral cue consisted of a pair of leftward and rightward arrowheads flanking the fixation dot, each starting 0.6° from the fixation point and composed of two 0.5°-long \times 0.12°-wide black lines 92° apart (Fig. 1A). The attentional cue was either a leftward

arrowhead indicating a reference angle of 30° or 60°, or a rightward arrowhead indicating 120° or 150°, depending on the reference combination for that block (Fig. 1B top). For the practice blocks and the testing sessions, the feedback was a 1°-long \times 0.06°-wide line on top of a white fixation dot (radius 0.15°) presented at the reference angle of the just-perceived stimulus, to remind observers of the exact reference orientations. For all training sessions, the feedback was given at the fixation dot indicating trial

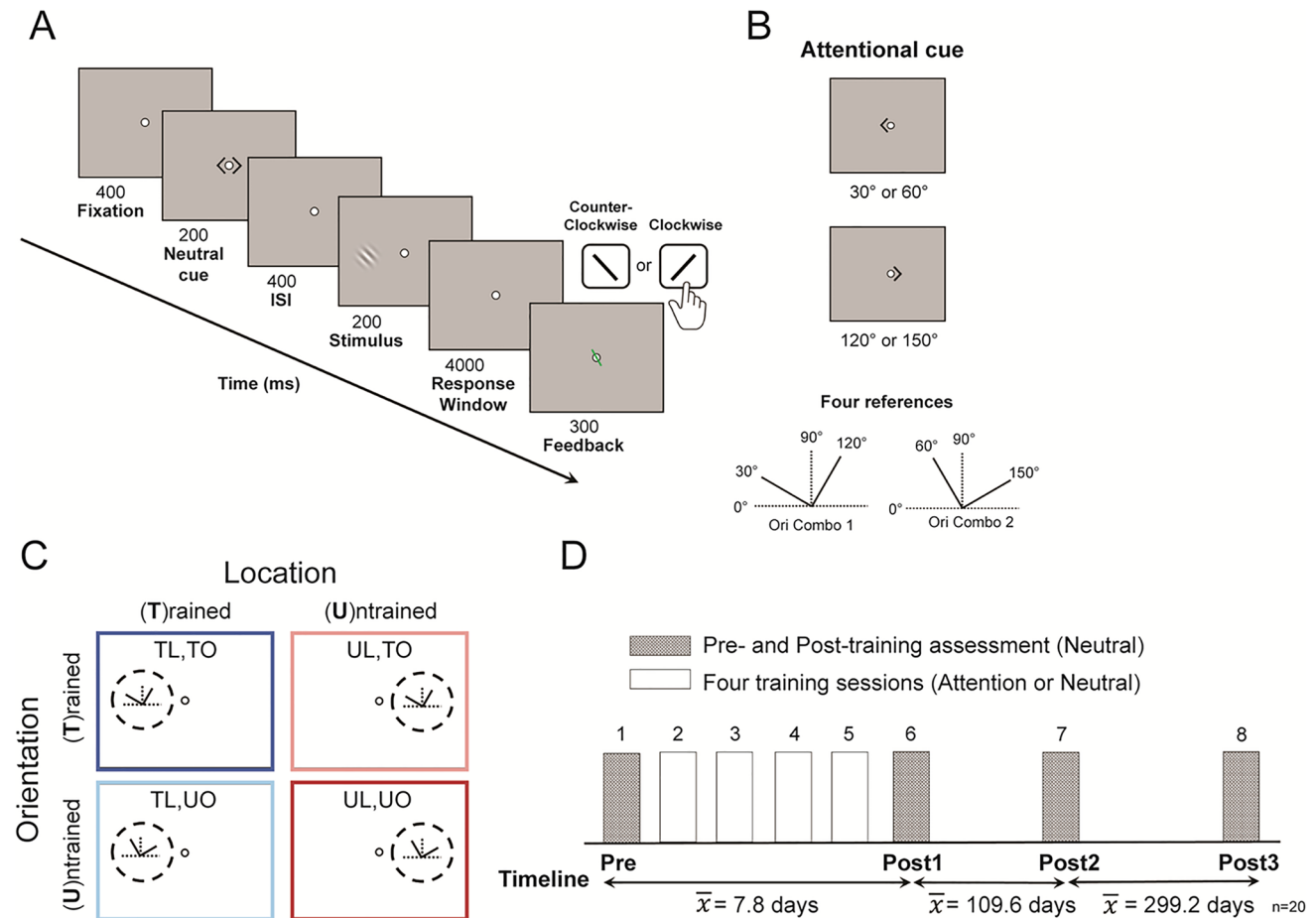


Fig. 1 Illustration of the orientation discrimination task and design of the visual perceptual learning study. **(A)** Each trial began with a fixation period of 400 ms followed by a 200-ms cue (neutral or attention). After a 400-ms interstimulus interval (ISI), a Gabor stimulus was presented for a single interval of 200 ms, and the observer's task was to judge whether the orientation of the stimulus was counter-clockwise or clockwise relative to the closest reference orientation **(B bottom)** by pressing labeled keys “/” or “\” on the keyboard within 4 s (i.e., response window). A 300-ms feedback was given as a colored line flashing green for correct responses, or red for incorrect responses, presented at the reference angle of the just-perceived stimulus. **(B top)** Attentional cue. In the attention condition, the cue was either a leftward arrowhead indicating a reference angle of 30° or 60°, or a rightward arrowhead indicating 120° or 150°, depending on the reference combination in each block. **(B bottom)** Four reference orientations (either combination 1 of 30°/120°, or combination

2 of 60°/150°) indexed different features in this task. Before each block, one of the reference combinations was shown to observers, but never appeared on the screen during the stimulus presentation. **(C)** Trained and untrained conditions in the testing sessions. The dark blue, light blue, light red, and dark red panels represent trained location/orientation (TL, TO), trained location/untrained orientation (TL, UO), untrained location/trained orientation (UL, TO), and untrained location/orientation (UL, UO), respectively. **(D)** Schematic illustration of the 6-day VPL experiment. Observers were tested on day 1 (Pre-test) and day 6 (Post-test 1) and were trained with a neutral cue or an attention cue on days 2–5 depending on their assigned group. Observers performed an identical testing session 3–4 months (Post-test 2) and more than 1 year (Post-test 3) after completion of the VPL experiment to assess the long-term retention of training effects of perceptual learning

accuracy. The color of the feedback was shown as green for correct or red for incorrect responses.

Orientation discrimination task

Each trial began with a 400-ms fixation period followed by a 200-ms neutral or attentional cue (Fig. 1A). After a 400-ms ISI, the stimulus was presented for a single 200-ms interval, and the observer's task was to judge whether the orientation of the stimulus was clockwise or counter-clockwise to the closest reference orientation by pressing labeled keys “/” or “\” on the keyboard, respectively. We used four reference orientations (either reference combination 1 of 30°/120°, or combination 2 of 60°/150°), which indexed different features in this task (Fig. 1B bottom). The temporal parameters ensured that observers had time to deploy FBA (Liu et al., 2007). Before each block, two reference lines were shown to observers but never appeared on the screen during stimulus presentation, so observers were encouraged to use their internal templates to perform the orientation discrimination. Observers had 4 s to indicate their answer. After a key-press, they received a 300-ms feedback line flashing green for correct responses, or red for incorrect responses, presented at the reference angle of the just-perceived stimulus to remind them of the exact reference orientations. There was a 1-s interstimulus interval. Given the nature of simultaneous features in our design, and that no explicit reference was shown during orientation discrimination, this task was difficult even for experienced observers.

Practice

Before the experiment, observers completed 40 trials of a simple color-discrimination task to familiarize themselves with the procedure and timing, and to reduce procedural learning during the perceptual learning experiment. Then observers performed four practice blocks (20 trials each) of the orientation task, with reference combinations (30°/120° or 60°/150°) and locations (left or right) counterbalanced and a 10° offset between targets and references. The criterion was 70% accuracy before proceeding to the main task.

Experimental design

This was a 6-day perceptual learning experiment. Observers were tested at 5° eccentricity on the left or right horizontal meridian for each of the reference combinations – 30°/120° or 60°/150° – on their first and sixth days and completed four training sessions on days 2–5 (Fig. 1C, D). All six sessions were performed at the same or a similar time across the average time frame of 7.8 days ($SD = 1.5$ days), with ≤ 2 days between consecutive sessions (except one observer who completed in 13 days with a 3-day and a

4-day between-session gap). To isolate the effects of training with FBA on VPL, all observers were presented with a neutral cue during both their pre-test (before training) and post-test (after training) sessions.

The testing sessions consisted of 400 trials, all presented with a neutral cue, equally distributed between four different conditions (e.g., stimuli on the left or right, and reference orientations of 30°/120° or 60°/150°; Fig. 1C). Each of the four conditions contained two blocks of 50 trials (five trials per offset size and reference angle). The order of the eight blocks was randomized. During the training sessions, observers performed one condition for 800 trials, with 400 trials for each reference orientation, with a neutral or attention cue depending on the group assignment. To use the attention cue in the Attention group (Fig. 1B top), observers were instructed to deploy their attention to a particular feature (orientation) indexed by the cue before the stimulus presentation. The 800 trials were split into 16 blocks of 50 trials (five trials per offset size and reference angle), with short breaks between blocks and a 5-min break in the middle of the session. In addition, to assess how long the training effects would last, all observers from the two groups were recruited back 3–4 months after completion of the 6-day experiment and asked to perform the same testing session (i.e., Post-test 2; Fig. 1D). Moreover, six observers from the Neutral group and six observers from the Attention group were re-tested 1 year after completion of the six-day experiment (i.e., Post-test 3; Fig. 1D). Due to the COVID-19 pandemic, we could not recruit the rest of the observers.

Data analysis

Behavioral data analysis

Performance in the orientation discrimination task was measured using the method of constant stimuli (across five orientation offsets). Observer performance in each condition was plotted as psychometric curves across five orientation offsets, and threshold was estimated by a power function ($f(x) = ax^n$, where a is a constant and n is a real number) where observers achieved 75% accuracy. The performance changes at post-tests were calculated as $(\text{Threshold}_{\text{pre}} - \text{Threshold}_{\text{post}}) / \text{Threshold}_{\text{pre}}$ for each observer and represented as Mean Percent Improvement (MPI) in Fig. 2. Error bars in Fig. 2 represent ± 1 within-subject SE (Cousineau, 2005). Figures 1 and 2 have been reported in Hung and Carrasco (2021).

Microsaccade detection

Online eye-tracking was employed throughout the experiment. If an eye-movement outside of the 2° radius fixation window or a blink was detected at any point after the

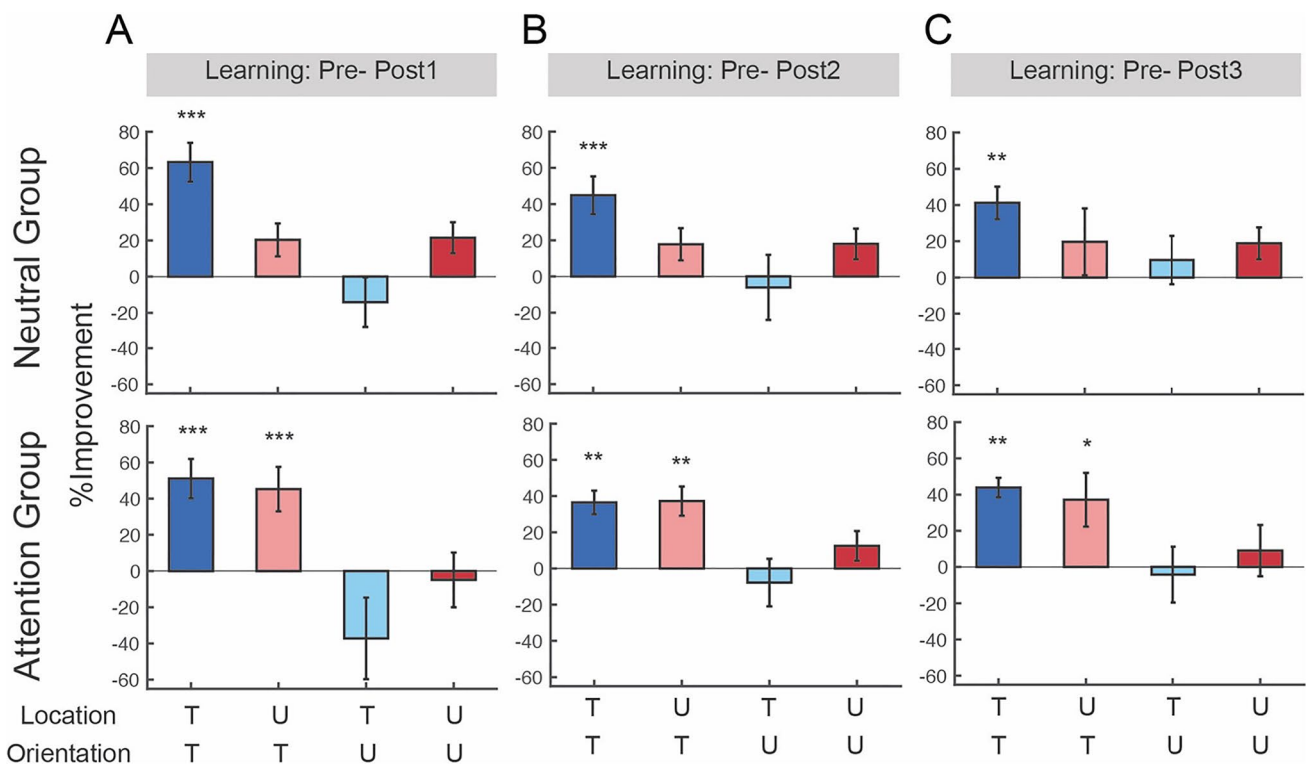


Fig. 2 Performance changes between the Neutral and Attention groups in perceptual learning. **(A)** Performance changes between Pre-test and Post-test 1. Both Neutral and Attention groups showed significant learning in the trained condition (**top & bottom**, dark blue bars). Contrary to the Neutral group, training with feature-based attention (FBA) overcame location specificity (**bottom**, light red bar), while preserving orientation specificity (**bottom**, light blue, dark red bars). **(B)** Performance changes between Pre-test and Post-test 2. Consistent with the results in Post-test 1, the improvement in both

groups (**top and bottom**, dark blue bars) and location transfer in the Attention group (**bottom**, light red bar) were preserved 3–4 months after completion of training. **(C)** Performance changes between Pre-test and Post-test 3. The improvement in both groups (**top and bottom**, dark blue bars) and location transfer induced by FBA (**bottom**, light red bar) persisted longer than 1 year after training. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Error bars represent ± 1 within-subject SEM (Cousineau, 2005)

trial started until the stimulus offset, that trial was aborted and repeated at the end of each block. Raw gaze positions recorded by an Eyelink 1000 eye tracker were converted to degrees of visual angle using the data from a nine-point calibration at the beginning of each session. The first 50 ms of the fixation window was discarded in the analyses to avoid an initial artifact when extracting microsaccades. Blinks were identified based on the Eyelink built-in algorithm, and blink intervals – 100 ms before the blink onset and 150 ms after the blink offset – were excluded from the saccade analysis. Saccades were detected using a standard velocity-based algorithm (Engbert & Kliegl, 2003), in which the detection thresholds were determined in two-dimensional (2D) velocity space computed separately for horizontal and vertical components. The threshold per trial was set such that a saccade onset was defined as the point in which its velocity exceeded this trial's median velocity by 6 or more standard deviations, for a minimum duration of 6 ms. An intersaccadic interval (between the saccade offset and the next saccade onset) of 10 ms was imposed to prevent detection of

overshoots, which sometimes follow saccade offsets and may be erroneously detected as a new saccade. As saccades and microsaccades fell along the main sequence (i.e., saccade amplitudes and peak velocities are highly correlated), lying along the “microsaccade-saccade continuum” (Otero-Millan et al., 2011; Rucci & Poletti, 2015), we defined microsaccades as saccades with an amplitude smaller than 1° of visual angle (Abeles et al., 2020; Badde et al., 2020; Martinez-Conde et al., 2013). The onset, offset, amplitude, peak velocity, and direction of each microsaccade were recorded.

Microsaccade analysis

To analyze microsaccade distributions across trials, microsaccades were binned based on microsaccade onset within a particular trial segment (e.g., FIX, CUE, ISI) identified by trial markers. The whole trial sequence was split into six segments – fixation period (FIX, 350 ms), cue presentation (CUE, 200 ms), interstimulus interval (ISI, 400 ms), stimulus presentation (STIM, 200 ms),

response window (RESPW, time varied across trials and observers), and the post response window (POST RESPW, 600 ms). The percentage of microsaccades for each condition was calculated as the number of microsaccades within a trial segment normalized by each observer's total number of microsaccades across the trial over Pre-test and Post-test 1 (Fig. 3).

For each observer and session, microsaccade rate per second for the entire trial sequence was calculated by averaging the number of microsaccades per time point (1 ms) across all trials in each session and multiplying these values by the sampling rate (1,000 Hz). The microsaccade-rate time course was then smoothed by applying a sliding Gaussian window of 50 ms (Figs. 4, 5 and 6).

To assess microsaccade directionality, we binned microsaccades in 12 directions with the middle of the directional bins centered on the horizontal and vertical meridians on polar histograms (Figs. 7 and 8). We collapsed data across Pre-test, Post-test 1, and Post-test 2. The proportion of microsaccades in each direction bin was normalized based on the total number of microsaccades within each trial segment. For directionality analysis based on the stimulus location, direction of all stimulus-on-right trials was normalized as if the stimulus had been presented on the left visual field (0° on polar histograms). For directionality analysis based on the stimulus features, direction of all trials at reference combination of $60^\circ/150^\circ$ was normalized as if the stimulus had been presented at the $30^\circ/120^\circ$ reference combination.

Statistics

For the behavioral results in the orientation discrimination task, we conducted a three-way ANOVA with within-subject factors of condition (trained vs. untrained) and training (Pre-test vs. Post-test 1), and a between-subjects factor of group (neutral vs. attention) using discrimination threshold values to examine potential interactions between the two groups. When a three-way interaction was found, a two-way ANOVA (condition \times training) was conducted to assess the threshold changes after training for each group. Paired t-tests were used to assess the performance changes for each condition within each group (Fig. 2).

To assess microsaccade timeseries differences between conditions and across observers in the data, we performed a cluster-based permutation test, which is a nonparametric statistical test that corrects for multiple comparisons at individual time points and determines whether an observed effect is greater than expected by chance (Maris & Oostenveld, 2007). To compare the timeseries difference between two conditions (e.g., Pre-test vs. Post-test 1) across observers, we used a two-sided cluster-based permutation test in which (positive or negative) t-values were derived from each time point individually and then obtained clusters comprising contiguous below-threshold ($p < 0.05$) time points. For each permutation iteration, we took the largest cluster mass, which is the largest of the summed absolute t-values within a cluster. We shuffled

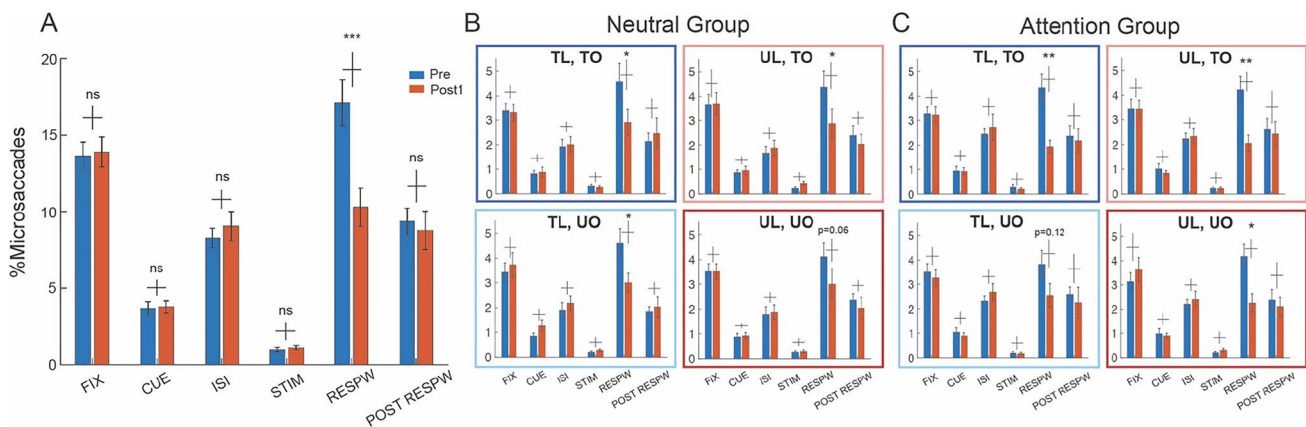


Fig. 3 Across-trial comparisons of microsaccade distributions of Pre-test versus Post-test 1. **(A)** The percentage (%) of microsaccades was calculated as the number of microsaccades within a trial segment normalized by each observer's total number of microsaccades across the trial over Pre-test and Post-test 1. Microsaccade distribution was comparable in all the trial segments (FIX, CUE, ISI, STIM, and POST RESPW) between Pre-test (blue bars) and Post-test 1 (orange bars), except for the response window (RESPW). Microsaccade per-

centage was greatly reduced in Post-test 1 during the response window (shown in asterisks). This pattern of results was the same for the **(B)** Neutral group and the **(C)** Attention group across the trained and untrained conditions. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Error bars represent ± 1 within-subject SEM. Vertical bars above paired comparisons represent ± 1 SEM for the mean percentage difference between Pre-test and Post-test 1

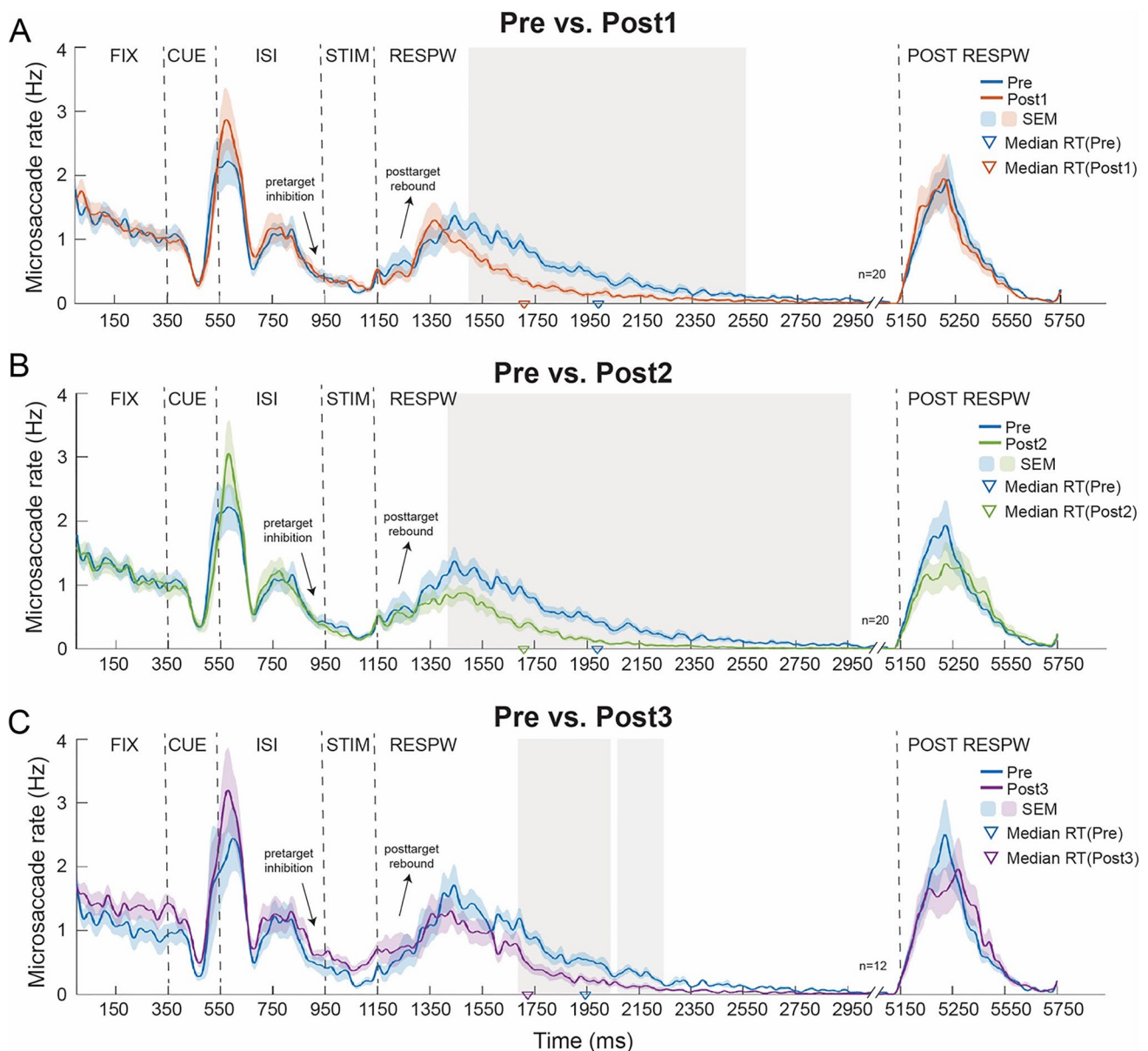


Fig. 4 Long-lasting reduction of microsaccade rates during the response window after training. Temporal dynamics of the microsaccade rates between Pre-test and Post-test 1 (**A**), Post-test 2 (**B**), and Post-test 3 (**C**). Data are combined across two groups. (**A**) Results from a cluster-permutation test revealed a significant cluster during the response window (gray-shaded area, $p < 0.001$), showing that the microsaccade rate was greatly decreased after training (Post-test 1, orange line). (**B**, **C**) The reduction of microsaccade rates during the response window remained 3–4 months (**B**, gray-shaded area, p

< 0.001) and more than 1 year (**C**, gray-shaded area, $p < 0.01$, and lightly gray-shaded area, $p = 0.055$) after completion of the VPL experiment, indicating long-lasting changes of microsaccade rates. Colored lines and shadings represent mean and ± 1 SEM for each testing session. Inverted triangles represent median response times (RTs) for each testing session. The significant time cluster emerged earlier than the median RT in all sessions, indicating that post-training microsaccade-rate changes were not driven by observers' shorter response times after training

the condition labels for each observer and repeated the same process 1,000 times. The largest cluster mass from each permuted dataset thus formed a null distribution of cluster sizes, and we defined a cluster in the data as

significant if an observed cluster mass was greater than 95% in the null distribution ($p < 0.05$), while controlling for the false alarm rate for all clusters.

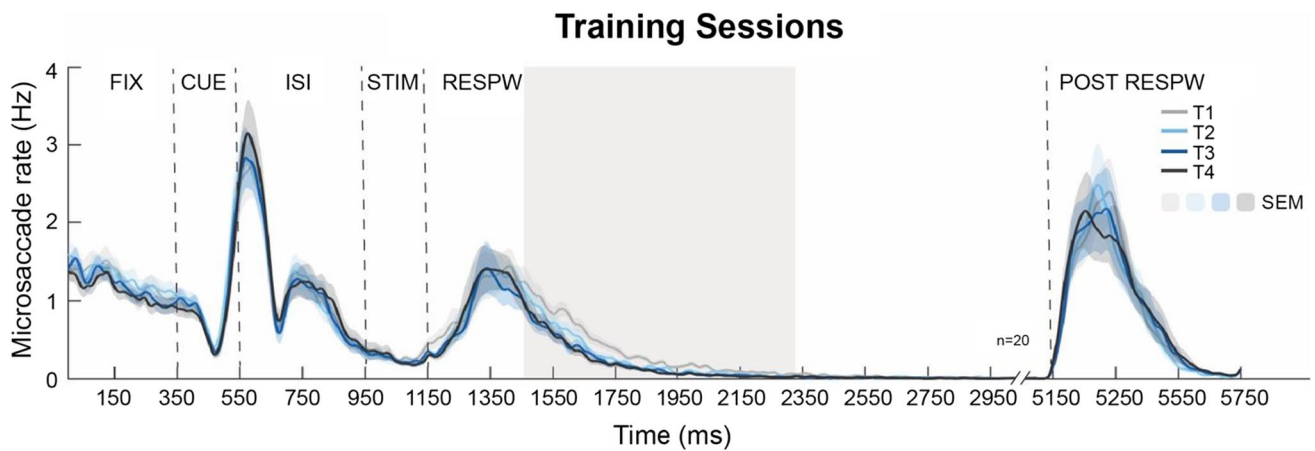


Fig. 5 Reduction of microsaccade rates emerged during training. Temporal dynamics of the microsaccade among the four training sessions (T1–T4). Comparison between T1 and T4 revealed a significant cluster during the response window (gray-shaded area, $p < 0.001$),

indicating that the reduction of microsaccade rate gradually emerged during training. Colored lines and shadings represent mean and ± 1 SEM for each training session

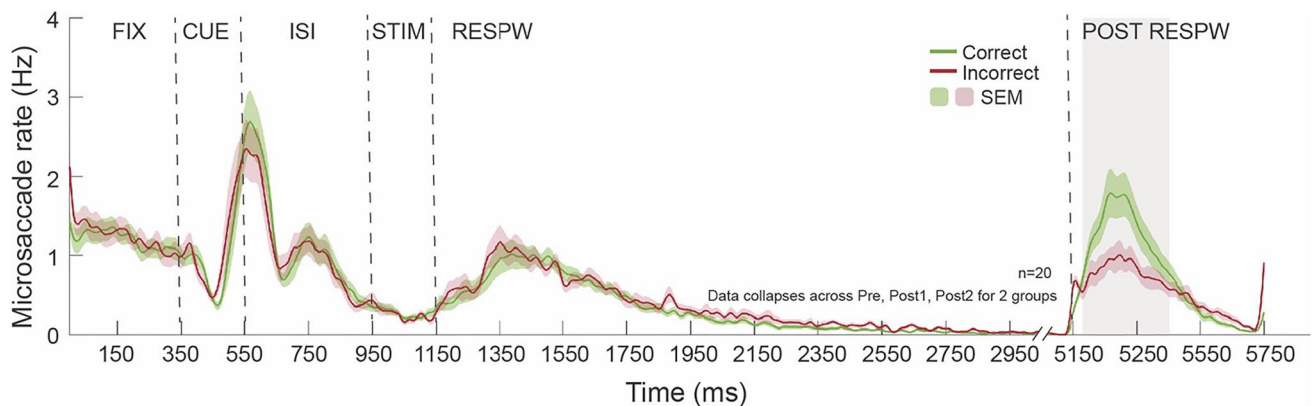


Fig 6 Microsaccade rate and trial accuracy. Temporal dynamics of the microsaccade rates between the correct (green line) and incorrect (red line) trials. Data are combined across Pre-test, Post-test 1 and Post-test 2 for two groups. The microsaccade rate was further suppressed for incorrect trials versus correct trials after observers pressed

a key response, when they were receiving feedback (gray-shaded area, $p < 0.001$). Colored lines and shadings represent mean and ± 1 SEM for each trial type

Results

Behavior

Observers participated in a 6-day VPL study. Observers in both the Attention and Neutral groups were presented with neutral cues during both the pre-test and post-test sessions which assessed their performance at two stimulus locations and two reference combinations (Fig. 1C). During the four training sessions, the Attention group was trained with a feature attention cue (Fig. 1B top) and the Neutral group with an uninformative cue (Fig. 1A). To assess long-term retention of training effects, observers were re-tested 3–4 months (Post-test 2), and 1 year (Post-test 3) after training

(Fig. 1D). The behavior results (Figs. 1 and 2) have been reported in Hung and Carrasco (2021).

After training, both groups of observers showed significant Mean Percent Improvement (MPI) at the trained orientations at the trained location (Fig. 2A top, dark blue bar = $63.2 \pm 10.7\%$, $t_8 = 20.035$, $p < 0.001$, Cohen's $d = 9.444$; Fig. 2A bottom, dark blue bar = $51.1 \pm 10.9\%$, $t_8 = 8.273$, $p < 0.001$, Cohen's $d = 3.9$, two-tailed, paired t-tests). The Neutral group showed location and orientation specificity: Learning in the orientation discrimination task did not transfer to any of the three untrained conditions (Fig. 2A top, light red bar = $20.3 \pm 9.1\%$, $t_8 = 1.279$, $p = 0.237$; light blue bar = $-14.1 \pm 13.7\%$, $t_8 = -0.684$, $p = 0.514$; and dark red bar = $21.5 \pm 8.6\%$, $t_8 = 1.716$, $p = 0.125$). In contrast, the

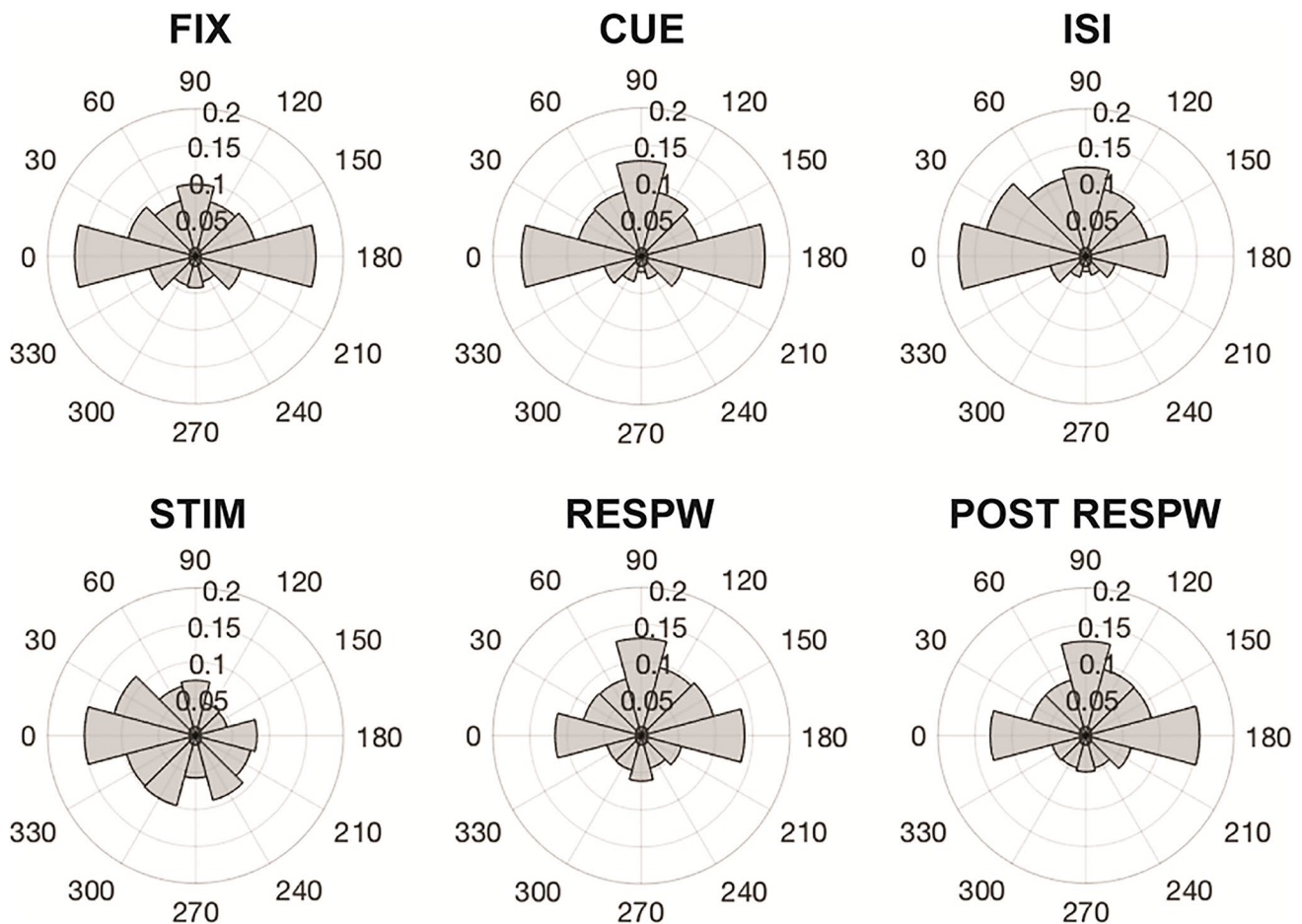


Fig. 7 Microsaccade directionality by stimulus location. Polar histograms of all trial segments. Data are combined across Pre-test, Post-test 1, and Post-test 2 for two groups. A typical horizontal bias was found most prominent during the fixation (FIX) and cue (CUE) periods. Also, an upward bias was observed in nearly all trial segments

except during the stimulus presentation (STIM). Importantly, the microsaccade direction was biased toward the stimulus location (normalized at 0° on polar histograms) during interstimulus interval (ISI), before the stimulus presentation, indicating an anticipatory effect of stimulus timing and location on the oculomotor system

Attention group showed complete learning transfer to the untrained location in the other hemifield (Fig. 2A bottom, light red bar = $45.3 \pm 12.3\%$, $t_8 = 7.112$, $p < 0.001$, Cohen's $d = 3.353$), with a comparable magnitude of performance change to the trained condition (Fig. 2A bottom, dark blue and light red bars, $t_8 = 0.617$, $p = 0.555$). Such transfer did not occur either at the untrained orientation for the trained location (Fig. 2A bottom, light blue bar = $-37.2 \pm 22.5\%$, $t_8 = -0.564$, $p = 0.266$), or at the untrained orientation and untrained location (Fig. 2A bottom, dark red bar = $-4.9 \pm 15.1\%$, $t_8 = -0.105$, $p = 0.829$).

Learning at the trained condition remained for both groups in Post-test 2 (Fig. 2B top, dark blue bar = $44.8 \pm 10.5\%$, $t_8 = 6.425$, $p < 0.001$, Cohen's $d = 3.029$; Fig. 2B bottom, dark blue bar = $36.5 \pm 6.5\%$, $t_8 = 4.312$, $p = 0.001$, Cohen's $d = 2.033$, one-tailed, paired t-tests), as well as in Post-test 3 (Fig. 2C top, dark blue bar = $41.2 \pm 9.0\%$, $t_5 = 3.859$, $p = 0.006$, Cohen's $d = 2.223$; Fig. 2C

bottom, dark blue bar = $43.8 \pm 5.4\%$, $t_4 = 4.27$, $p = 0.006$, Cohen's $d = 2.707$). Critically, in the Attention group, learning transfer was retained at the untrained location for the trained orientation in both Post-test 2 (Fig. 2B bottom, light red bar = $37.2 \pm 8.1\%$, $t_8 = 4.47$, $p = 0.001$, Cohen's $d = 2.107$) and Post-test 3 (Fig. 2C bottom, light red bar = $37.1 \pm 14.9\%$, $t_4 = 2.302$, $p = 0.041$, Cohen's $d = 1.456$). No transfer was found in the other untrained conditions in either the Neutral group (Fig. 2C top, $p = 0.497$ for light red bar, $p = 0.529$ for light blue bar, and $p = 0.309$ for dark red bar) or the Attention group (Fig. 2C bottom, $p = 0.868$ for light blue bar, and $p = 0.736$ for dark red bar). Therefore, our behavioral results revealed remarkable location transfer induced by FBA, reminiscent of its global effect across the visual field (Herrmann et al., 2012; Maunsell & Treue, 2006; Saenz et al., 2002; Serences & Boynton, 2007; White & Carrasco, 2011; White et al., 2015; Zhang & Luck, 2009). Furthermore, the improvements in the

trained condition in both groups and the location transfer in the Attention group were preserved for over a year, indicating robust and long-term benefits when trained with FBA in VPL.

Microsaccade distribution

To investigate the role of microsaccades in VPL, we first analyzed the microsaccade distribution across the trial before and after the training sessions. Microsaccades ($< 1^\circ$ fixational eye movements) were detected using a standard velocity-based algorithm (Engbert & Kliegl, 2003) and followed the main sequence (Fig. S1 (Online Supplemental Material (OSM))), i.e., microsaccade amplitude and peak velocity are highly correlated, Pearson's $r = 0.93$, $p < 0.001$ across observers.

We found that microsaccade distribution was comparable in most trial segments before and after training, except for the response window (Fig. 3A), in which the microsaccade percentage was greatly reduced in Post-test 1 (asterisks in Fig. 3A), when observers were trying to give a key response after perceiving the stimulus. We collapsed data across groups and conditions because the reduction of microsaccades was consistent across the trained and untrained conditions for both groups (Figs. 3B, C), and deploying FBA did not significantly affect the microsaccade temporal pattern either during or after training. Furthermore, the reduction of microsaccades was not correlated with the performance improvement at the trained condition ($p > 0.1$). A three-way mixed ANOVA with within-subject factors of training (Pre-test vs. Post-test 1) and condition (trained vs. untrained), and a between-subjects factor of group (Neutral vs. Attention) using microsaccade percentages in the response window showed a significant main effect of training ($F(1,18) = 17.639$, $p < 0.001$). But there was no main effect of condition ($F < 1$), neither a significant three-way interaction among training, condition and group ($F(3,54) = 1.670$, $p = 0.184$). To exclude the possibility that the post-training reduction of microsaccades was due to a shorter response time, we analyzed the microsaccade-rate time course (in Hz) across observers which precisely reflects the emergence of microsaccade change.

Baseline microsaccade temporal dynamics

Overall, the pattern of microsaccade-rate time course exhibited expected dynamics across the trial sequence (Fig. 4). After initializing the fixation period, the microsaccade rate briefly dipped following a visual cue (350–550 ms) from a rate of ~ 1.8 Hz to ~ 0.2 Hz (Badde et al., 2020; Denison et al., 2019; Engbert & Kliegl, 2003; Rolfs et al., 2005). The microsaccade rate bounced to 2–3 Hz at the beginning of the ISI, then gradually declined over the ISI window (550–950

ms) and was largely suppressed before the stimulus presentation (~ 950 ms) at a rate of ~ 0.5 Hz. This pattern is consistent with the literature showing oculomotor inhibition prior to a predictable target across sensory modalities (Abeles et al., 2020; Amit et al., 2019; Badde et al., 2020; Dankner et al., 2017; Denison et al., 2019). The clear “pretarget inhibition” of microsaccades indicates observers’ temporal expectation on stimulus presentation in our task. During the stimulus presentation (950–1,150 ms), the microsaccade rate was suppressed (~ 0.2 Hz), and this strong inhibition was followed by a typical rebound to a rate of ~ 1.5 Hz after the stimulus offset (“post-target rebound”), which appeared at the beginning of the response window (1,150–1,350 ms). After the post-target rebound, the microsaccade rate decreased slowly over the long response window (maximum 4 s) and rebounded again after observers made a key press in this task (5,150–5,350 ms).

Changes of microsaccade rate in VPL

To compare the microsaccade temporal dynamics before and after training, we performed a cluster-based permutation test (see *Data analysis: Statistics*) to assess the time-series difference of microsaccade rates between Pre-test and Post-test 1 (Fig. 4A, blue and orange lines, respectively). Because the microsaccade distribution across trial segments was comparable between the Neutral and Attention group (Fig. 3B and C), we combined data by averaging the time series of 20 observers. Results from this test revealed a significant cluster in the time window of 1,496–2,554 ms (Fig. 4A, gray-shaded area, $p < 0.001$), showing that the microsaccade rate decreased during the response window after training (Fig. 4A, orange line). Of note, the significant cluster started at 557 ms after the stimulus onset and was much earlier than the median response time of observers in Pre-test and Post-test 1, which were 1,040 ms and 758 ms, respectively (inverted triangles in Fig. 4A, also see Fig. S2A (OSM)). Thus, the fact that the microsaccade-rate difference of Pre-test versus Post-test 1 emerged early during the response time window ruled out the possibility that these learning-related changes were due to a shorter response time after training. Additionally, results from the training sessions showed that the microsaccade rate was gradually reduced during the response window along with training (Fig. 5, gray-shaded area, $p < 0.001$). This post-training reduction was found irrespective of the microsaccade amplitude (Fig. S3 (OSM), $< 0.5^\circ$ or 0.5 – 1°). There were no learning-related changes in the microsaccade amplitude in any trial segment (Fig. S4 (OSM)). Overall, these results indicate that these microsaccadic changes in rate were tightly coupled with VPL and could serve as its reliable physiological correlate.

Given that our behavioral findings revealed long-term retention of training benefits, we examined whether the

learning-related microsaccade-rate difference was also long lasting. All 20 observers were re-tested in the same orientation discrimination task 3–4 months (110 ± 26 days) after their Post-test 1, which we called Post-test 2. Similar to Post-test 1, we observed that microsaccade-rate timeseries was reduced during the response window in Post-test 2 (Fig. 4B, green line). Results from the cluster-based permutation test revealed that microsaccade-rate timeseries of Post-test 2 significantly differed from Pre-test in the time window of 1,417–2,961 ms (Fig. 4B, gray-shaded area, $p < 0.001$). The significant time cluster starting at 602 ms after the stimulus onset appeared earlier than the median response time in Post-test 2 (758 ms, green inverted triangle in Fig. 4B, also see Fig. S2B (OSM)), and further confirmed that post-training microsaccade-rate changes were not resultant from observers' shorter response time after training. In addition, comparison of Post-test 1 versus Post-test 2 showed no significant cluster(s) in microsaccade-rate timeseries (Fig. S5 (OSM)).

A consideration is whether observers' pattern of eye blinks – which often took place during the response window – would affect our microsaccade-rate results, as blinks are highly associated with microsaccades (Costela et al., 2014; Khazali et al., 2017). Given that our analyses spanned a long trial period including a response window up to 4 s, observers often blinked after the stimulus offset during the response window, a time when fixation was not enforced, and observers could freely move their eyes. In any case, to address this possibility, we removed all trials in which any eye blink(s) occurred during the entire trial sequence and repeated the microsaccade-rate analyses for all pre-test and post-test sessions. Although removing trials with eye blinks led to a loss of 25% observers (with the criterion that any observer losing $> 60\%$ data on average across three testing sessions was excluded, $n = 5$) in our dataset, our findings still remained (Fig. S6 (OSM)). The microsaccade rates significantly decreased during the response window after training (Fig. S6A), and this learning-induced reduction in microsaccade rates remained after 3–4 months in Post-test 2 (Fig. S6B). Thus, our findings and conclusions are resilient to the pattern of observers' eye blinks.

Moreover, to assess the training effects over a longer time scale, 12 observers were re-tested one year (412 ± 33 days) after completion of training, which we called Post-test 3 (due to the COVID-19 pandemic, we could not test the rest of observers). Although we had lower number of observers in Post-test 3 (Fig. 4C, purple line), comparison of microsaccade-rate timeseries in Pre-test versus Post-test 3 still revealed one significant cluster and one near-significant cluster in the following response time windows: 1,688–2,041 ms (Fig. 4C, gray-shaded area, $p < 0.01$) and 2,067–2,244 ms (Fig. 4C, lightly gray-shaded area, $p = 0.055$), respectively. Also, comparisons of Post-test 1 versus Post-test 2 (Fig. S7A (OSM)), and Post-test 1 versus Post-test 3 (Fig. S7B (OSM))

showed no significant cluster(s) in microsaccade-rate timeseries. Taken together, the results showed that the microsaccade rates robustly decreased during the response window across the post-test sessions over a long-time scale, in line with our behavioral findings showing long-lasting training benefits in VPL.

Microsaccade rate and trial accuracy

Task demands modulate the characteristics of microsaccades (Ko et al., 2010; Rucci & Poletti, 2015; Winterson & Collewijn, 1976): microsaccades tend to be less frequent during the execution of a high-acuity visuomotor task, such as threading a needle, than during sustained fixation. Additionally, microsaccade rates were lower in correct than incorrect trials shortly before and after the target (Badde et al., 2020). Here, we investigated whether and how the microsaccade rate is influenced by trial accuracy in an orientation discrimination task by analyzing the microsaccade-rate time course across trial when observers responded correctly versus incorrectly.

We found that the microsaccade-rate timeseries was comparable for correct versus incorrect trials in most of the trial segments, except in the post response window (Fig. 6). Because the change of microsaccade rate in the post response window was consistent both in the pre-test and post-test sessions across two groups, we collapsed data across Pre-test, Post-test 1, and Post-test 2 for both Neutral and Attention groups. The microsaccade rate was further suppressed for incorrect trials (at a rate of ~ 1 Hz) than for correct trials (at a rate of ~ 2 Hz) after observers pressed a key response, when they were receiving feedback regarding the accuracy of their responses. Results from the cluster-based permutation test revealed a significant time cluster from 5,179–5,450 ms (Fig. 6, gray-shaded area, $p < 0.001$). Given that we presented not only accuracy but also an accurate reference angle of the just-shown stimulus as feedback in this challenging task, the stronger inhibition of microsaccade rate in incorrect trials could reflect observers' attempt to gather precise information about the feature from the feedback while fixating.

Microsaccade directionality

To explore the role of microsaccade directionality, we assessed whether observers had any directional bias toward the target location and feature across the trial sequence (Figs. 7 and 8). Data were combined across Pre-test, Post-test 1, and Post-test 2 for both groups. We first analyzed the microsaccade directionality by stimulus location. The polar histograms showed a typical horizontal bias that was most prominent during the fixation and cue periods (Fig. 7) (Denison et al., 2019; Engbert & Kliegl, 2003). In addition

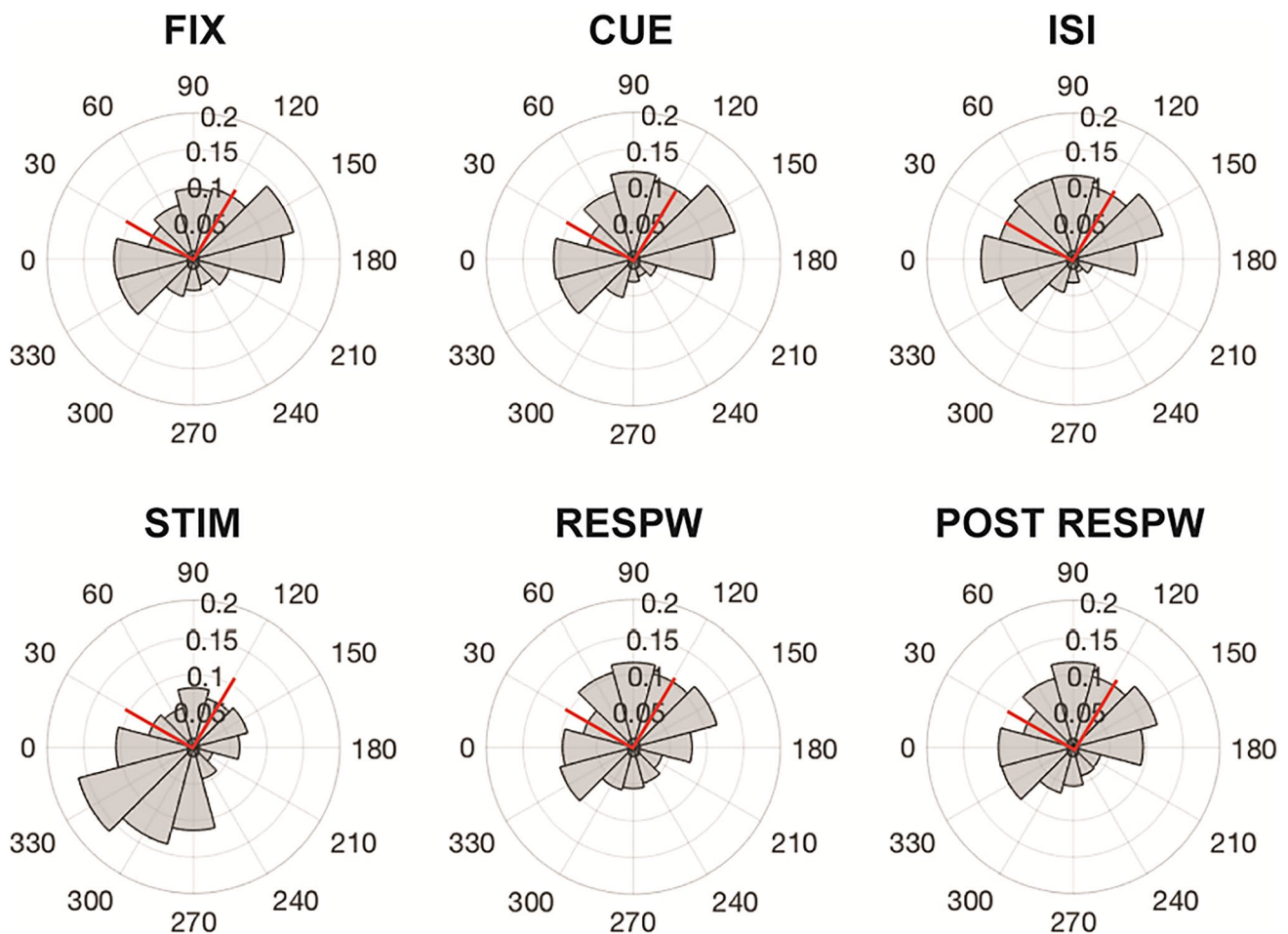


Fig. 8 MS directionality by stimulus feature. Polar histograms of all trial segments. Data are combined across Pre-test, Post-test 1, and Post-test 2 for two groups. Stimulus features were normalized at 30°/120° (marked as red lines on polar histograms). An upward bias was observed in nearly all trial segments, with a slight diagonal skew

along the 150°–330°. Directionality during the stimulus presentation (STIM) exhibited a diagonal skew toward the lower left visual field. No directional bias toward the stimulus features (normalized at 30°/120°, marked as red lines) was found in any trial segment

to the horizontal bias, we also observed an upward bias in nearly all trial segments except during the stimulus presentation. Importantly, we found that the microsaccade direction was biased toward the stimulus location (normalized at 0° on polar histograms) during ISI, before the stimulus presentation. The directional bias toward the stimulus location, together with the “pretarget inhibition” of microsaccade rate prior to the stimulus, indicate an anticipatory effect of stimulus timing and location on the oculomotor system in our task.

In terms of the microsaccade directionality by stimulus feature, we also observed an upward bias in nearly all trial segments, with a slight diagonal skew along the 150°–330° axis (Fig. 8). Unlike the other trial segments, directionality during the stimulus presentation exhibited a diagonal skew toward the lower left visual field. We did not find the directional bias toward the stimulus features normalized at 30°/120° (marked as red lines on polar histograms) in any trial segment.

Discussion

Training with FBA induces location transfer in VPL in an orientation discrimination task, and the training benefits attained both at the trained and transfer locations persist over 1 year (Hung & Carrasco, 2021). Consistent with the VPL literature, the Neutral group exhibited location and orientation specificity. The location transfer induced by FBA is consonant with the psychophysical and neural evidence that FBA effects are independent of the location of the attended stimuli (Herrmann et al., 2012; Maunsell & Treue, 2006; Saenz et al., 2002; Serences & Boynton, 2007; White & Carrasco, 2011; White et al., 2015; Zhang & Luck, 2009). That study (Hung & Carrasco, 2021) expands our understanding of FBA’s global modulation from human visual perception to VPL, and provide converging evidence that, as with spatial attention (Donovan & Carrasco, 2018; Donovan et al., 2015,

2020; Roberts & Carrasco, 2022), deploying covert attention is a powerful tool to potentiate VPL benefits by enabling location transfer.

Here we discovered that VPL modulates fixational eye movements. VPL induced a long-lasting reduction of microsaccade rates, specifically during the trial's response window, and such reduction emerged gradually during training. Also, microsaccade rates were further suppressed in incorrect trials after observers' responses, which could reflect observers' attempts to gather precise information from the feedback, as the reference angle was displayed. Additionally, we found a directional bias toward the target location, specifically prior to the target onset, indicating an anticipatory effect of stimulus timing and location on the oculomotor system. All these results were highly similar for the observers who trained with FBA and those who trained in a neutral condition.

Why was the decrease of microsaccade rates associated with VPL specific to the response window while observers were preparing for a key response? Voluntary control can affect both microsaccades and saccades (Ko et al., 2010; Willeke et al., 2019) as their neural generation circuits largely overlap. Also, visual working memory engages the oculomotor system (van Ede et al., 2019). The hippocampus and associated medial temporal lobe (MTL) structures, which are critical in learning and memory, are intricately connected with the oculomotor system (Meister & Buffalo, 2016), including the superior colliculus, a primary region involved in microsaccade generation (Hafed & Krauzlis, 2010). In a memory-guided microsaccade task, both monkey and human observers voluntarily generate microsaccades based on foveal visual working memory (Willeke et al., 2019). Thus, the decrease of microsaccade rates during the response window show that microsaccades may play a functional role during retrieval and reformation of visual representations in VPL.

Notably, the observed microsaccade-rate changes during the response window were found in the trained and the untrained conditions for both groups (Fig. 3B, C). This overall effect indicates that the learning-induced microsaccade changes generalized to untrained locations and features regardless of whether or not observers trained with FBA. This finding is consistent with the fact that silencing of saccade suppression, which is specific to an expected time window, generalizes to untrained stimuli (Scholes et al., 2021) after training in a visual detection task. Thus, the reduction of microsaccade rates could serve as a reliable learning marker in VPL across trained/untrained conditions in a highly rhythmic task.

Reweighting models have proposed VPL as a multi-level learning system that involves higher-level, location-/feature-independent representations and lower-level, location-/feature-dependent representations (Doshier et al., 2013; Doshier & Lu, 2017). Whereas

learning specificity is mediated by reweighting the location-/feature-dependent representations, transfer arises from increasing the weights between the location/feature-independent representations and the decision unit. The changes of microsaccade-rate pattern across trained/untrained conditions may reflect neurophysiological modifications in higher-level cortical areas during supervised learning (i.e., when feedback is provided), likely between location-/feature-independent representations and the decision unit.

Studies of temporal expectation in which correct and incorrect responses have been analyzed in the pre- and post-target intervals, have yielded inconsistent results: an auditory study reported no differences between correct and incorrect trials (Abeles et al., 2020), whereas in a tactile study, microsaccade rates were lower in correct than incorrect trials (Badde et al., 2020). In the present study, the microsaccade rates in the pre- and post-target intervals were comparable between the correct and incorrect trials. Interestingly, the microsaccade rate significantly decreased after observers' responses (key-press) when they responded incorrectly than correctly. This finding is consonant with studies showing that microsaccades tend to be less frequent in a highly demanding task than during sustained fixation (Ko et al., 2010; Rucci & Poletti, 2015). Because we presented a feedback line at the exact reference angle of the just-shown stimulus in this challenging task, the lower microsaccade rate could reflect observers' attempt to gather precise feature information from the feedback, especially after an incorrect response.

In conclusion, the present study is the first to investigate microsaccades in VPL and the long-term retention of VPL effects on the oculomotor system. The finding that the microsaccade rate was dynamically changed during the response window reveals a unique function of fixational eye movements in retrieving and reforming stable representations in VPL. Further, microsaccades in a gaze-contingent task could serve as a reliable physiological marker reflecting long-term learning changes. Together with studies investigating VPL before (Rolfs et al., 2018) and during (Porat & Zohary, 2016; Rolfs et al., 2018; Scholes et al., 2021) saccades, this study provides evidence of tight links between VPL and oculomotor processes. To obtain a complete picture of VPL mechanisms and maximize training and translational benefits (Lu et al., 2016), further research should investigate the interactions of visual and oculomotor systems and how a broad network of brain processes jointly contribute to behavioral learning effects.

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Author Contributions S.-C. Hung and M. Carrasco conceived and designed the study. S.-C. Hung performed the experiments and analyzed data. S.-C. Hung and M. Carrasco interpreted the data and wrote the paper.

Declarations

Conflict of Interest The authors declare no competing financial interests.

Open Practices Statement The data that support the findings of this study are available from the corresponding author upon reasonable request. The experiments were not preregistered.

References

- Abeles, D., Amit, R., Tal-Perry, N., Carrasco, M., & Yuval-Greenberg, S. (2020). Oculomotor inhibition precedes temporally expected auditory targets. *Nature Communications*, *11*(1), 3524. <https://doi.org/10.1038/s41467-020-17158-9>
- Amit, R., Abeles, D., Carrasco, M., & Yuval-Greenberg, S. (2019). Oculomotor inhibition reflects temporal expectations. *NeuroImage*, *184*, 279–292. <https://doi.org/10.1016/j.neuroimage.2018.09.026>
- Badde, S., Myers, C. F., Yuval-Greenberg, S., & Carrasco, M. (2020). Oculomotor freezing reflects tactile temporal expectation and aids tactile perception. *Nature Communications*, *11*(1), 3341. <https://doi.org/10.1016/j.neuroimage.2018.09.026>
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. Retrieved from <https://www.ncbi.nlm.nih.gov/pubmed/9176952>
- Cavanaugh, M. R., Barbot, A., Carrasco, M., & Huxlin, K. R. (2019). Feature-based attention potentiates recovery of fine direction discrimination in cortically blind patients. *Neuropsychologia*, *128*, 315–324. <https://doi.org/10.1016/j.neuropsychologia.2017.12.010>
- Cavanaugh, M. R., Tadin, D., Carrasco, M., & Huxlin, K. R. (2022). Benefits of endogenous spatial attention during visual double-training in cortically-blinded fields. *in press*.
- Costela, F. M., Otero-Millan, J., McCamy, M. B., Macknik, S. L., Troncoso, X. G., Jazi, A. N., et al. (2014). Fixational eye movement correction of blink-induced gaze position errors. *PLoS One*, *9*(10), e110889. <https://doi.org/10.1371/journal.pone.0110889>
- Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorial in Quantitative Methods for Psychology*, *1*. <https://doi.org/10.20982/tqmp.01.1.p042>
- Dankner, Y., Shalev, L., Carrasco, M., & Yuval-Greenberg, S. (2017). Prestimulus inhibition of saccades in adults with and without attention-deficit/hyperactivity disorder as an index of temporal expectations. *Psychological Science*, *28*(7), 835–850. <https://doi.org/10.1177/0956797617694863>
- Denison, R. N., Yuval-Greenberg, S., & Carrasco, M. (2019). Directing voluntary temporal attention increases fixational stability. *The Journal of Neuroscience*, *39*(2), 353–363. <https://doi.org/10.1523/JNEUROSCI.1926-18.2018>
- Deveau, J., Ozer, D. J., & Seitz, A. R. (2014). Improved vision and on-field performance in baseball through perceptual learning. *Current Biology*, *24*(4), R146–R147. <https://doi.org/10.1016/j.cub.2014.01.004>
- Donovan, I., & Carrasco, M. (2018). Endogenous spatial attention during perceptual learning facilitates location transfer. *Journal of Vision*, *18*(11), 7. <https://doi.org/10.1167/18.11.7>
- Donovan, I., Szpiro, S., & Carrasco, M. (2015). Exogenous attention facilitates location transfer of perceptual learning. *Journal of Vision*, *15*(10), 11. <https://doi.org/10.1167/15.10.11>
- Donovan, I., Shen, A., Tortarolo, C., Barbot, A., & Carrasco, M. (2020). Exogenous attention facilitates perceptual learning in visual acuity to untrained stimulus locations and features. *Journal of Vision*, *20*(4), 18. <https://doi.org/10.1167/jov.20.4.18>
- Doshier, B. A., & Lu, Z. L. (2017). Visual perceptual learning and models. *Annual Review of Vision Science*, *3*, 343–363. <https://doi.org/10.1146/annurev-vision-102016-061249>
- Doshier, B. A., Jeter, P., Liu, J., & Lu, Z. L. (2013). An integrated reweighting theory of perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(33), 13678–13683. <https://doi.org/10.1073/pnas.1312552110>
- Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research*, *43*(9), 1035–1045. [https://doi.org/10.1016/s0042-6989\(03\)00084-1](https://doi.org/10.1016/s0042-6989(03)00084-1)
- Furmanski, C. S., Schluppeck, D., & Engel, S. A. (2004). Learning strengthens the response of primary visual cortex to simple patterns. *Current Biology*, *14*(7), 573–578. <https://doi.org/10.1016/j.cub.2004.03.032>
- Hafed, Z. M., & Krauzlis, R. J. (2010). Microsaccadic suppression of visual bursts in the primate superior colliculus. *The Journal of Neuroscience*, *30*(28), 9542–9547. <https://doi.org/10.1523/JNEUROSCI.1137-10.2010>
- Herrmann, K., Heeger, D. J., & Carrasco, M. (2012). Feature-based attention enhances performance by increasing response gain. *Vision Research*, *74*, 10–20. <https://doi.org/10.1016/j.visres.2012.04.016>
- Hung, S. C., & Carrasco, M. (2021). Feature-based attention enables robust, long-lasting location transfer in human perceptual learning. *Scientific Reports*, *11*(1), 13914. <https://doi.org/10.1038/s41598-021-93016-y>
- Hung, S. C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *The Journal of Neuroscience*, *34*(25), 8423–8431. <https://doi.org/10.1523/JNEUROSCI.0745-14.2014>
- Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America*, *88*(11), 4966–4970. <https://doi.org/10.1073/pnas.88.11.4966>
- Karni, A., & Sagi, D. (1993). The time course of learning a visual skill. *Nature*, *365*(6443), 250–252. <https://doi.org/10.1038/365250a0>
- Khazali, M. F., Pomper, J. K., & Thier, P. (2017). Blink associated resetting eye movements (BARMs) are functionally complementary to microsaccades in correcting for fixation errors. *Scientific Reports*, *7*(1), 16823. <https://doi.org/10.1038/s41598-017-17229-w>
- Ko, H. K., Poletti, M., & Rucci, M. (2010). Microsaccades precisely relocate gaze in a high visual acuity task. *Nature Neuroscience*, *13*(12), 1549–1553. <https://doi.org/10.1038/nn.2663>
- Levi, D. M., & Li, R. W. (2009). Perceptual learning as a potential treatment for amblyopia: A mini-review. *Vision Research*, *49*(21), 2535–2549. <https://doi.org/10.1016/j.visres.2009.02.010>
- Liu, T., Stevens, S. T., & Carrasco, M. (2007). Comparing the time course and efficacy of spatial and feature-based attention. *Vision Research*, *47*(1), 108–113. <https://doi.org/10.1016/j.visres.2006.09.017>

- Lu, Z. L., Lin, Z., & Doshier, B. A. (2016). Translating perceptual learning from the laboratory to applications. *Trends in Cognitive Sciences*, 20(8), 561–563. <https://doi.org/10.1016/j.tics.2016.05.007>
- Maniglia, M., & Seitz, A. R. (2018). Towards a whole brain model of perceptual learning. *Current Opinion in Behavioral Sciences*, 20, 47–55. <https://doi.org/10.1016/j.cobeha.2017.10.004>
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron*, 49(2), 297–305. <https://doi.org/10.1016/j.neuron.2005.11.033>
- Martinez-Conde, S., Otero-Millan, J., & Macknik, S. L. (2013). The impact of microsaccades on vision: Towards a unified theory of saccadic function. *Nature Reviews Neuroscience*, 14(2), 83–96. <https://doi.org/10.1038/nrn3405>
- Maunsell, J. H., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, 29(6), 317–322. <https://doi.org/10.1016/j.tins.2006.04.001>
- McCamy, M. B., Otero-Millan, J., Macknik, S. L., Yang, Y., Troncoso, X. G., Baer, S. M., ... Martinez-Conde, S. (2012). Microsaccadic efficacy and contribution to foveal and peripheral vision. *The Journal of Neuroscience*, 32(27), 9194–9204. <https://doi.org/10.1523/JNEUROSCI.0515-12.2012>
- Meister, M. L. R., & Buffalo, E. A. (2016). Getting directions from the hippocampus: The neural connection between looking and memory. *Neurobiology of Learning and Memory*, 134 Pt A, 135–144. <https://doi.org/10.1016/j.nlm.2015.12.004>
- Otero-Millan, J., Macknik, S. L., Serra, A., Leigh, R. J., & Martinez-Conde, S. (2011). Triggering mechanisms in microsaccade and saccade generation: A novel proposal. *Annals of the New York Academy of Sciences*, 1233, 107–116. <https://doi.org/10.1111/j.1749-6632.2011.06177.x>
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, 10(4), 437–442. Retrieved from <https://www.ncbi.nlm.nih.gov/pubmed/9176953>
- Porat, Y., & Zohary, E. (2016). Practice improves peri-saccadic shape judgment but does not diminish target mislocalization. *Proceedings of the National Academy of Sciences of the United States of America*, 113(46), E7327–E7336. <https://doi.org/10.1073/pnas.1607051113>
- Roberts, M., & Carrasco, M. (2022). Exogenous attention generalizes location transfer of perceptual learning in adults with amblyopia. *iScience*, 25(3), 103839. <https://doi.org/10.1016/j.isci.2022.103839>
- Rolfs, M., Engbert, R., & Kliegl, R. (2005). Crossmodal coupling of oculomotor control and spatial attention in vision and audition. *Experimental Brain Research*, 166(3–4), 427–439. <https://doi.org/10.1007/s00221-005-2382-y>
- Rolfs, M., Murray-Smith, N., & Carrasco, M. (2018). Perceptual learning while preparing saccades. *Vision Research*, 152, 126–138. <https://doi.org/10.1016/j.visres.2017.11.009>
- Rucci, M., & Poletti, M. (2015). Control and functions of fixational eye movements. *Annu Rev Vis Sci*, 1, 499–518. <https://doi.org/10.1146/annurev-vision-082114-035742>
- Rucci, M., Iovin, R., Poletti, M., & Santini, F. (2007). Miniature eye movements enhance fine spatial detail. *Nature*, 447(7146), 851–854. <https://doi.org/10.1038/nature05866>
- Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, 5(7), 631–632. <https://doi.org/10.1038/nn876>
- Sagi, D. (2011). Perceptual learning in vision research. *Vision Research*, 51(13), 1552–1566. <https://doi.org/10.1016/j.visres.2010.10.019>
- Scholes, C., McGraw, P. V., & Roach, N. W. (2021). Learning to silence saccadic suppression. *Proceedings of the National Academy of Sciences of the United States of America*, 118(6). <https://doi.org/10.1073/pnas.2012937118>
- Schoups, A. A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412(6846), 549–553. <https://doi.org/10.1038/35087601>
- Serences, J. T., & Boynton, G. M. (2007). Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*, 55. <https://doi.org/10.1016/j.neuron.2007.06.015>
- van Ede, F., Chekroud, S. R., & Nobre, A. C. (2019). Human gaze tracks attentional focusing in memorized visual space. *Nature Human Behaviour*, 3(5), 462–470. <https://doi.org/10.1038/s41562-019-0549-y>
- White, A. L., & Carrasco, M. (2011). Feature-based attention involuntarily and simultaneously improves visual performance across locations. *Journal of Vision*, 11(6). <https://doi.org/10.1167/11.6.15>
- White, A. L., Rolfs, M., & Carrasco, M. (2015). Stimulus competition mediates the joint effects of spatial and feature-based attention. *Journal of Vision*, 15(14), 7. <https://doi.org/10.1167/15.14.7>
- Willeke, K. F., Tian, X., Buonocore, A., Bellet, J., Ramirez-Cardenas, A., & Hafeed, Z. M. (2019). Memory-guided microsaccades. *Nature Communications*, 10(1), 3710. <https://doi.org/10.1038/s41467-019-11711-x>
- Winterson, B. J., & Collewijn, H. (1976). Microsaccades during finely guided visuomotor tasks. *Vision Research*, 16(12), 1387–1390. [https://doi.org/10.1016/0042-6989\(76\)90156-5](https://doi.org/10.1016/0042-6989(76)90156-5)
- Xue, C., Calapai, A., Krumbiegel, J., & Treue, S. (2020). Sustained spatial attention accounts for the direction bias of human microsaccades. *Scientific Reports*, 10(1), 20604. <https://doi.org/10.1038/s41598-020-77455-7>
- Yan, F. F., Zhou, J., Zhao, W., Li, M., Xi, J., Lu, Z. L., & Huang, C. B. (2015). Perceptual learning improves neural processing in myopic vision. *Journal of Vision*, 15(10), 12. <https://doi.org/10.1167/15.10.12>
- Yashar, A., & Carrasco, M. (2016). Rapid and long-lasting learning of feature binding. *Cognition*, 154, 130–138. <https://doi.org/10.1016/j.cognition.2016.05.019>
- Yashar, A., Chen, J., & Carrasco, M. (2015). Rapid and long-lasting reduction of crowding through training. *Journal of Vision*, 15(10), 15. <https://doi.org/10.1167/15.10.15>
- Yotsumoto, Y., Watanabe, T., & Sasaki, Y. (2008). Different dynamics of performance and brain activation in the time course of perceptual learning. *Neuron*, 57(6), 827–833. <https://doi.org/10.1016/j.neuron.2008.02.034>
- Yuval-Greenberg, S., Merriam, E. P., & Heeger, D. J. (2014). Spontaneous microsaccades reflect shifts in covert attention. *The Journal of Neuroscience*, 34(41), 13693–13700. <https://doi.org/10.1523/JNEUROSCI.0582-14.2014>
- Zhang, W., & Luck, S. J. (2009). Feature-based attention modulates feedforward visual processing. *Nature Neuroscience*, 12(1), 24–25. <https://doi.org/10.1038/nn.2223>

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