Perceptual learning while preparing saccades

Martin Rolfs[a,b,c,d,*], Nicholas Murray-Smith[c], Marisa Carrasco[c,d]

[a] Department of Psychology, New York University, NY, USA
[b] Center for Neural Science, New York University, NY, USA
[c] Department of Psychology, Humboldt-Universität zu Berlin, Germany
[d] Bernstein Center for Computational Neuroscience, Humboldt-Universität zu Berlin, Germany

ARTICLE INFO

ABSTRACT

Traditional perceptual learning protocols rely almost exclusively on long periods of uninterrupted fixation. Taking a first step towards understanding perceptual learning in natural vision, we had observers report the orientation of a briefly flashed stimulus (clockwise or counterclockwise from a reference orientation) presented strictly during saccade preparation at a location offset from the saccade target. For each observer, the saccade direction, stimulus location, and orientation remained the same throughout training. Subsequently, we assessed performance during fixation in three transfer sessions, either at the trained or at an untrained location, and either using an untrained (Experiment 1) or the trained (Experiment 2) stimulus orientation. We modeled the evolution of contrast thresholds (i.e., the stimulus contrast necessary to discriminate its orientation correctly 75% of the time) as an exponential learning curve, and quantified departures from this curve in transfer sessions using two new, complementary measures of transfer costs (i.e., performance decrements after the transition into the Transfer phase). We observed robust perceptual learning and associated transfer costs for untrained locations and orientations. We also assessed if spatial transfer costs were reduced for the remapped location of the pre-saccadic stimulus—the location the stimulus would have had (but never had) after the saccade. Although the pattern of results at that location differed somewhat from that at the control location, we found no clear evidence for perceptual learning at remapped locations. Using novel, model-based ways to assess learning and transfer costs, our results show that location and feature specificity, hallmarks of perceptual learning, subsist if the target stimulus is presented strictly during saccade preparation throughout training.

1. Introduction

Vision develops across the lifespan, and in many visual tasks, performance improves with practice even in adults. Such perceptual learning alters fundamental visual abilities, including spatial resolution in high-acuity tasks, contrast sensitivity, motion detection, and discrimination of basic perceptual dimensions (e.g., Ball & Sekuler, 1982; Fahle & Edelman, 1993; Fiorentini & Berardi, 1980, 1981; Jeter, Dosher, Petrov, & Lu, 2009; Yu, Klein, & Levi, 2004). Understanding the learning mechanisms that enable and shape the acquisition of perceptual competence has been a major research program extending over several decades (reviews in W. Li, 2016; Lu, Hua, Huang, Zhou, & Dosher, 2011; Sagi, 2011; Sasaki, Nanez, & Watanabe, 2009), and its results promise ways to ameliorate deficits in patients facing perceptual challenges (e.g., Cavanaugh et al., 2015; Das, Tadin, & Huxlin, 2014; Polat, Ma-Naim, Belkin, & Sagi, 2004; see Deveau & Seitz, 2014; Levi & Li, 2009; Levi & Polat, 1996; Lu, Lin, & Dosher, 2016 for reviews).

The vast majority of studies in this field have focused on experimental contexts in which sequences of hundreds of visual stimuli are presented during prolonged fixation. Whereas this approach has proven useful at isolating key aspects of perceptual learning, such as location specificity (see below), it has ignored a potential impact of active visual behavior. Indeed, eye movements form a vital part of natural vision in humans and other primates (Findlay & Gilchrist, 2003)—about 10,000 saccades rapidly shift fixation every waking hour. An important goal, therefore, should be to understand perceptual learning under natural conditions—during active vision—in which learners actively employ motor behavior as they acquire new perceptual skills. Yet, the number of studies that has explored the relation between perceptual learning and eye movements can be counted on the fingers of one hand (Szpiro, Spering, & Carrasco, 2014; Zhang & Li, 2010; Zhang, Zhang et al., 2013). In particular, no study thus far has explored the validity of key features of perceptual learning—as they have been established in traditional protocols—for stimuli presented around the time of saccadic eye movements. In the present study, we took a first step to fill this gap and, in turn, probe the usefulness of

perceptual learning as a tool to address open questions in the realm of active vision.

A key signature of perceptual learning is its specificity: performance benefits resulting from training with a certain type of stimulus (e.g., rightward tilted bars presented to the right of fixation) do not usually transfer to other locations (left of fixation), other features along the trained dimension (e.g., leftward tilted bars), or to untrained feature dimensions (e.g., motion direction, spatial frequency, or color). The degree of this specificity—and thus the magnitude of transfer to other situations—varies with a range of factors, including task difficulty (Ahissar & Hochstein, 1997), the precision required in the task (Jeter et al., 2009), attention (Donovan, Szpiro, & Carrasco, 2015), and the training protocol (Wang, Zhang, Klein, Levi, & Yu, 2014; Xiao et al., 2008). In the endeavor to pinpoint the mechanisms underlying perceptual learning, understanding the conditions that yield specificity has been the focus of many studies (Li, 2016; Lu et al., 2011; Sagi, 2011). Beyond establishing if perceptual learning occurs when stimuli are presented in the temporal vicinity of a saccade, a second major goal of this study was to assess if under such condition it shows its hallmark spatial and feature specificity.

It is not obvious that spatially and feature specific learning can be induced by pre-saccadic stimuli. Indeed, psychophysical experiments tell us that vision undergoes turbulent changes every time the eye is about to move to a new location. In particular, when a saccade is imminent, observers experience spatial mislocalization of flashed stimuli (Honda, 1989; Lappe, Awater, & Krekelberg, 2000; Matin & Pearce, 1965; Ross, Morrone, & Burr, 1997) and notable reductions in visual sensitivity across the visual field (Burr, Morrone, & Ross, 1994; Dorr & Bex, 2013; Volkmann, Riggs, White, & Moore, 1978). At the same time, sensitivity at the target of the eye movement rapidly increases leading up to the execution of a saccade (Li, Barbot, & Carrasco, 2016; Rolfs & Carrasco, 2012), at the expense of other locations (Deubel, 2008; Montagnini & Castet, 2007; Ohl, Kuper, & Rolfs, 2017). In a process called predictive remapping, these performance benefits are updated just before the eyes move to a new location, and shift—in anticipation of the consequences of the eye movement—to the post-saccadic retinotopic location of the attended object (Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013; Puntiroli, Kerzel, & Born, 2015; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Szinte, Carrasco, Cavanagh, & Rolfs, 2015; Szinte, Jonikaitis, Rolfs, Cavanagh, & Deubel, 2016). These attention shifts may enable the visual system to instantly integrate information across different retinal locations (Ganmor, Landy, & Simoncelli, 2015; Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015), and establish long-term associations between poorly resolved visual features in the periphery with their high-resolution foveal versions across saccadic eye movements (Cox, Meier, Oertelt, & DiCarlo, 2005; Herwig & Schneider, 2014; Herwig, Weiss, & Schneider, 2015; Valsecchi & Gegenfurtner, 2016). This associative learning process differs from perceptual learning in several ways: it biases perception rather than making it more accurate, and it shows transfer to completely untrained locations (Valsecchi & Gegenfurtner, 2016). Indeed, the fact that eye movements place the same objects on different parts of the retina within a fraction of a second indeed raises the question how ecologically relevant spatial specificity of perceptual learning is.

If we suppose that perceptual learning occurs before saccades, such that the visual system establishes long-term performance benefits for specific features in specific retinotopic locations, then we could use this phenomenon to address a question that has so far been rather elusive: If the visual system predicts the post-saccadic location of a relevant object and shifts attention there (Rolfs et al., 2011), does it anticipate the features of the stimulus to arrive at that location as well? Previous attempts at answering this question have relied on other visual mechanisms that are both spatially and feature specific, such as visual adaptation (Biber & Ilg, 2011; He, Mo, & Fang, 2017; Melcher, 2007), crowding (Harrison, Retell, Remington, & Mattingley, 2013), masking (Hunt & Cavanagh, 2011), or feature integration (Szinte et al., 2016).

The earlier adaptation studies have been challenged by subsequent work (see Marino & Mazer, 2016 for review), in part, because they tested a different location than the target of predictive remapping (He et al., 2017; Rolfs et al., 2011). A recent re-investigation of predictive remapping of tilt adaptation did find evidence for an impact of an adapted feature (tilt) on the pre-saccadic remapped location of the adaptor (He et al., 2017). This feature prediction, however, may be explained most parsimoniously as a high-level expectation of what the target would look like (Paeye, Collins, & Cavanagh, 2017), rather than a transfer of neural adaptation from one set of neurons to another. All other studies cited above have yielded inconclusive results with respect to the question of feature remapping, because the reported feature-dependent consequences of remapping could be explained in terms of predictive remapping of spatial attention (e.g., Hunt & Cavanagh, 2011; Pelli & Cavanagh, 2013; Szinte et al., 2016).

Here, we adapted a fine orientation-discrimination task in which performance is known to benefit from perceptual learning and that reliably exhibits transfer costs (i.e., performance decrements observed in Transfer tests that indicate the specificity of learning) for untrained locations or orientations (Jeter et al., 2009). Participants judged the orientation of a briefly presented stimulus (discrimination target, DT; Fig. 1) relative to an implicit reference presented before each block. Visual performance was quantified as the contrast of the discrimination target (DT) needed to perform at 75% correct. We assessed changes in these contrast thresholds across eight 1-h sessions. Critically, in the Training phase (sessions 1 through 5), we presented each DT in an interval in which the observers prepared a saccade to another location. In the Transfer phase (sessions 6 through 8), observers were required to maintain fixation, and we tested performance either at the trained or at an untrained location, and either with an untrained orientation (Experiment 1), or the orientation practiced in the Training phase (Experiment 2). Importantly, we used a between-subject design: Each observer was trained while performing the same saccade on every trial of the Training phase, and tested in only 1 combination of DT location and orientation in the Transfer phase. Finally, we modeled observers' improvement in the Training phase as an exponential decrease in contrast threshold, and quantified transfer costs after the switch from the Training to the Transfer phase as a deviation from that learning curve.

Using this approach, we pursued the three research questions described above: (1) Does perceptual learning occur when stimuli are presented around the time of a saccade? (2) Is learning specific to the retinotopic location of the DT and the feature value used in the training phase? (3) Are transfer costs reduced at the remapped location of the attended DT and if so, is that transfer specific to the trained feature? To foreshadow the results: We found conclusive evidence for the first two questions, but not for the third.

2. Materials and methods

2.1. Participants

We recruited participants from within NYU as well as the surrounding community, through advertisements around campus, as well as postings on departmental and public websites. After a screening test (see below), 128 participants (18–42 years, $M = 24.2$ years; 68 female; 110 right-handed, 16 left-handed, and 2 ambidextrous) volunteered to enter the complete study of 8 sessions total and started the Training sessions. A subset of these participants dropped out before completing the study (N = 28), due to scheduling problems or other personal problems. Moreover, we discontinued running participants after the second session (N = 49) of the main experiment if their performance remained below 70% correct in the perceptual task. Due to the challenging nature of this task (a fine orientation-discrimination task on a noisy stimulus that was briefly flashed in the visual periphery while observers planned a saccadic eye movement to a different location; see below), many observers were not capable of achieving this high
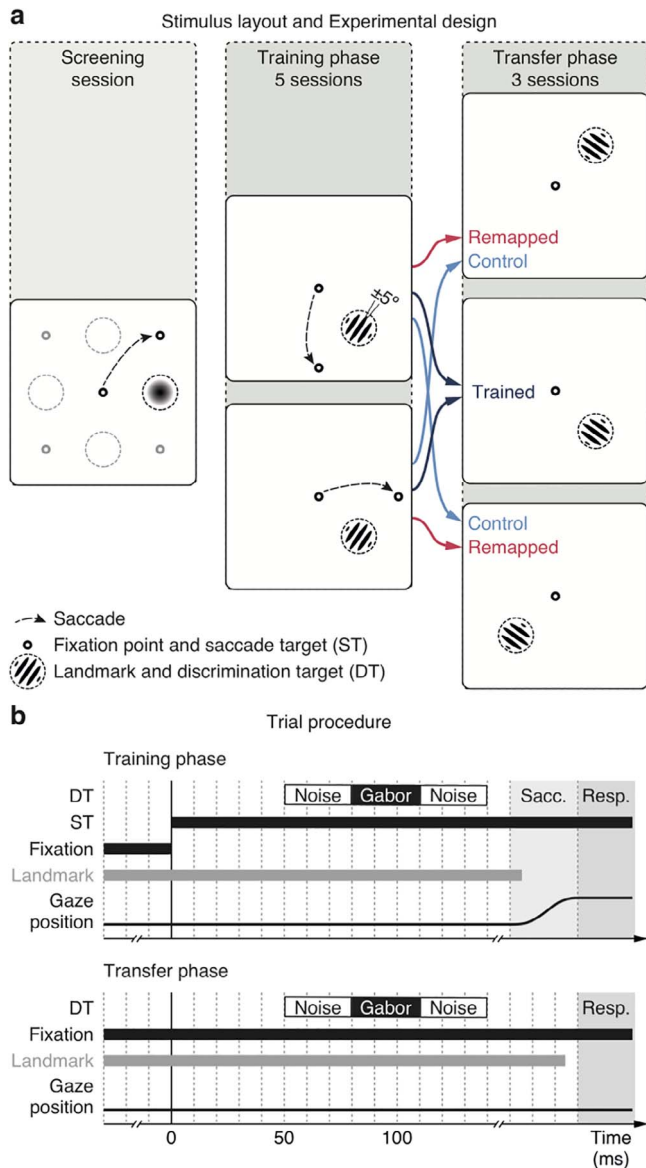
Fig. 1. Experimental procedure. a Stimulus layout and experimental design. Observers were selected for the main experiment in a Screening session, in which a saccade task was combined with a luminance discrimination task. The main experiment consisted of 8 sessions. In the Training phase (5 sessions), participants rapidly shifted gaze to a saccade target (ST), placed either below or to the right of fixation, while an oriented discrimination target (DT) was flashed at a predefined location in the lower-right part of the screen. In the subsequent Transfer phase (3 sessions), observers maintained fixation and orientation discrimination performance was tested at either the same (Trained; lower-right quadrant) or at a new location. Transfer locations were either in the lower-left or the upper-right quadrant, thus coinciding with the Remapped location of the Training phase or a Control location, depending on the direction of the saccade that was used during the Training phase. b Stimulus timing in Training and Transfer tasks. The DT (oriented Gabor) always appeared 80 ms after the ST, and was temporally embedded in noise.

standard. In most psychophysical tasks, the experimenters can provide more training to some observers until they attain the desired performance level. This is not the case in perceptual learning. All participants were naïve to the purposes of the study and were not trained psychophysical observers.

The final sample consisted of 51 participants, 31 (18–33 years, $M = 23.2$ years, 18 female, 28 right-handed, 3 left-handed, and 0 ambidextrous) in Experiment 1 and 20 (18–36 years, 15 female, 17 right-handed, 2 left-handed, and 1 ambidextrous) in Experiment 2, who completed all eight sessions of the main experiment. All participants had normal or corrected-to-normal vision, were naïve as to the purposes

of the experiment, and were paid for their participation ($10 USD per session, and a bonus of $20 USD for completing all eight sessions of the main experiment). We informed potential participants of this procedure before their inclusion in the study; the experiments were undertaken with the understanding and written consent of all participants. The NYU Institutional Review Board approved the experimental protocol, and we performed the experiment in accordance with the Declaration of Helsinki (2008).

2.2. Apparatus

Participants sat in a silent and dimly lit room with their head positioned on a chin rest. We presented stimuli at a distance of 57 cm on a gamma-linearized 22-inch Sony GDM-F520 screen (1280 by 960 pixels, 100 Hz vertical refresh). An EyeLink 1000 Desktop Mount (SR Research, Ottawa, ON, Canada) monitored and recorded observers' gaze position. An iMac computer (Apple Inc., Cupertino, CA, USA) running MATLAB (Mathworks, Natick, MA, USA) with standard toolboxes (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997) controlled stimulus presentation and response collection. Auditory feedback was provided using standard desktop computer-speakers.

2.3. Procedure and design

This study was highly demanding for participants both in terms of the psychophysical task (difficult perceptual judgement while making a saccade to a different location) and the time invested (eight one-hour sessions, preferably on consecutive days, and within 10 days in any case). To select participants for the main study, therefore, we first invited them to a Screening session. These sessions were brief (lasting approximately 30 min), provided procedural training, and formed a key necessity for the study. They ensured that observers would meet three basic task requirements. First, the Eyelink system had to be able to reliably track the observer's gaze position. This was essential because the timing and control of stimulus presentation were contingent upon online gaze tracking. Second, the observer had to consistently be able to maintain fixation and accurately execute the required saccade within the allotted timeframe (see below). Third, the observer had to obtain a minimum accuracy of 60% in a luminance discrimination task. Observers who met these criteria were invited to continue on to sessions of the main experiments. Nevertheless, the coarse luminance discrimination task (which demanded little attention compared to the fine-orientation discrimination in the main experiments) was a liberal choice, allowing more participants to start the main experiments than were able to complete it (see *Participants*).

The main experiments (including Training and Transfer tasks) consisted of a total of eight 1 h-sessions. Each session started with 2 warm-up trials (10 in sessions 1 and 6), followed by four blocks of 156 trials each (with breaks interspersed), resulting in a total of 624 trials per day. In each trial of the first 5 sessions (Training task), observers performed a difficult orientation discrimination task at a fixed, peripheral location while preparing a saccade to a different, but also fixed location. After completing the 5 Training sessions, observers were tested in 3 Transfer sessions, in which we assessed performance at one of three peripheral locations.

As is typical in perceptual learning studies, we used a between-subjects design to be able to isolate the effects of the different training conditions. For all observers, the discrimination target (DT) location was the same during the Training phase: down and to the right of the initial fixation position. However, each observer was assigned to make saccades to one of two saccade target (ST) locations during the Training phase—either below or to the right of their initial fixation—and a single DT location in the Transfer phase: top-right, bottom-right or bottom-left. Thus, DT locations in the Transfer phase could correspond to the trained location, a remapped, or a control location, depending on the

direction of the saccade in the Training phase (see Fig. 1a). In Experiment 1, we assessed transfer costs in discrimination performance at these three locations after changing the DT orientation by 90°. In Experiment 2, instead, the DT had the same orientation in both the Training and the Transfer phase; any transfer costs, therefore, would result from a change in location only.

2.4. Stimuli and task

2.4.1. Screening task

The Screening task (Fig. 1a, left column) was procedurally similar to the main experiment: observers performed a speeded saccade and a concurrent perceptual judgement in the visual periphery. Timing and features of the stimuli were identical to those in the Training phase of the main experiment (see *Training task* below), with a few critical exceptions. First, the STs and DTs were located so as to avoid pre-training at any of the retinotopic locations relevant to the main experiment. STs were located at four equidistant locations along the 45° diagonals, while DTs were located at four equidistant locations along the horizontal and vertical meridians. Their eccentricities were identical to those in the main experiment. DTs always appeared at a location neighboring the saccade vector. In order to avoid orientation-specific training in the Screening session, and to ease people into the dual task situation with a less demanding perceptual task, we used a coarse luminance discrimination judgment on a Gaussian luminance patch of either dark or light pixels (diameter of 3 degrees of visual angle, dva; standard deviation of 0.4 dva) presented briefly between patches of external Gaussian noise (cf. *Training task*). As in the main experiment, saccades had to occur within a 400 ms interval after the movement cue; there was no time limit for the observers to make their manual response. Auditory feedback indicated incorrect responses (correct responses did not elicit a tone).

2.4.2. Training task

In each trial of the Training phase, observers prepared and executed a speeded saccade and then performed an orientation discrimination about a stimulus presented just before the onset of the saccade (Fig. 1a, middle column). The perceptual task was modeled after the "High Precision" condition in Jeter et al. (2009). These task parameters were chosen to insure a high degree of specificity. The goal was to measure the transfer cost at the trained location and compare it to the transfer costs at the untrained locations.

Observers judged oriented DTs: Gabor patches (sinusoidal gratings with 2 cycles per dva; random phase; windowed by a Gaussian function with a standard deviation of 0.4 dva) tilted either 5° clockwise or counter-clockwise relative to an implicit reference angle (35° clockwise relative to vertical). The reference angle was the same throughout the Training phase and was illustrated at the beginning of each block.

DTs could potentially range from 0.78 to 100% luminance contrast and the contrast level on a given trial was altered (i.e., incremented, left constant, or decremented) from trial to trial using adaptive staircase procedures. Two staircases were randomly interleaved: a 1-up/2-down staircase converging on 70.7% accuracy and a 1-up/3-down staircase which converges on 79.3% accuracy (Levitt, 1971). Step-size was fixed at 0.0458 log units.

Each trial in the Training phase (Fig. 1b) started with a fixation point (a red circle 0.2 dva diameter, centered in a black annulus, 0.7 dva in diameter) presented at the center of neutral grey background. A dashed circle (3 dva diameter) with its center 5.67 dva from fixation (4 dva rightward and 4 dva downward, relative to fixation) was also present, providing a landmark for the location where the DT would appear. Once eye-tracking registered the observer's gaze within 1 dva of the fixation point for 200 ms, the red circle disappeared and the trial began. After a variable delay period (350–550 ms), the fixation point was displaced by 8 dva, forming the ST and signaling to the observer to initiate a saccade. 50 ms later the DT appeared briefly, temporally

sandwiched in patches of Gaussian noise (30 ms Noise + 30 ms Gabor + 30 ms Noise). Once the observer completed their saccade they were provided as much time as needed to make their judgment and response. Incorrect responses were indicated by auditory feedback.

In both the Screening and Training sessions, any eye-movement errors resulted in the current trial being immediately aborted and discarded, with replacement trials inserted randomly at the end of the block. Events registering as eye-movement errors included premature breaks in fixation, inaccurate saccades (landing more than 2 dva from the center of the ST), failure to saccade within 400 ms of ST onset, and eye-movements beginning before the presentation of the DT (anticipatory saccades).

2.4.3. Transfer task

In the Transfer phase, observers maintained fixation and performed an orientation discrimination as in the Training phase; with identical stimulus timing (Fig. 1b). In Experiment 1, participants now judged a reference angle orthogonal to that in the Training task (55° counterclockwise relative to vertical), as we intended to have significant transfer costs (cf. Jeter et al., 2009). In Experiment 2, the reference angle remained the same as in the Training task (35° clockwise relative to vertical). In both experiments, the DT was located at the trained, the remapped or the control location (see Fig. 1a, right column) and remained at this location throughout the Transfer phase.

2.5. Data preprocessing

We low-pass filtered the eye position data offline and detected saccades based on their 2D-velocity. We computed smoothed eye velocities using a moving average over five subsequent 1 ms eye position samples in a trial (Engbert & Mergenthaler, 2006). Saccades exceeded the median velocity by 5 SDs for at least 8 ms. We merged events separated by 10 ms or less into a single saccade, as the algorithm often detects two saccades when the saccade overshoots at first. We defined response saccades as the first saccade leaving a fixation region and landing inside an area of 2 dva around the ST.

2.6. Data analyses: individual model fits

A total of 51 participants completed the experiment. In Experiment 1, one observer who had completed all eight sessions had to be excluded because the display had unintentionally been set to an incorrect resolution in the first session. Thus, 50 participants entered initial analyses (see Table 1 for a breakdown by experiment and condition). Each observer participated in eight sessions of 624 trials each: five sessions in the Training phase, in which DTs appeared during saccade preparation, and three sessions in the Transfer phase, in which DTs appeared during visual fixation. We adapted the luminance contrast of the DT on each trial, using a staircase procedure (see Supplementary information for an analysis of thresholds based on staircase reversals). Thus, in each session, we obtained an observer's reports (clockwise or counterclockwise with respect to a reference orientation) for a range of stimulus contrasts. To relate reports and stimulus contrast c, we fitted Gumbel (i.e., log-Weibull) functions to the data of each session:

$$\Psi(c;\theta,\beta,\lambda) = 0.5 + (0.5-\lambda)(1-e^{-10^{\beta(c-\theta)}}) \tag{1}$$

The function has three free parameters: a lapse rate λ, a slope β, and a threshold θ—our main dependent variable—that is, the contrast needed to achieve 50% of the observer's asymptotic performance $(1-\lambda)$.

Importantly, we fitted a model to each observer's entire data set (Kingdom & Prins, 2016; Prins & Kingdom, n.d.), estimating all sessions' thresholds at once. This allowed us to keep the slope and lapse rate constant across all sessions of a particular observer, and to benefit from more data entering the estimation of the function's parameters. More

Table 1
Number of observers per experiment and condition before and after data exclusion.

Transfer orientation	Transfer location	Saccade direction	# Observers completed	# Poor performance	# Extreme transfer costs	# Final sample
Orthogonal (Exp. 1)	Trained	Rightward	5	1	1	3
		Downward	4	2	1	2
	Remapped	Rightward	5	0	1	4
		Downward	4	0	0	4
	Control	Rightward	5	2	1	2
		Downward	7	1	2	4
Trained (Exp. 2)	Trained	Rightward	4	0	0	4
		Downward	3	1	0	2
	Remapped	Rightward	3	0	0	3
		Downward	4	0	1	3
	Control	Rightward	3	0	0	3
		Downward	3	0	0	3
Total			50	7	7	37

specifically, we first fitted a learning model to the data of the Training sessions of each individual (cf. Model I below), and obtained estimates of the lapse rate λ and the slope β that best described the individual's performance.

Next, we fixed the estimates of λ and β that we obtained in the first step, and fitted two alternative models of how thresholds may evolve over sessions. With $I_{Train} = \{1:5\}$ and $I_{Trans} = \{6:8\}$ referring to Training and Transfer sessions, respectively, the two models of how thresholds evolved over sessions were:

(I) Learning and no transfer costs (3 parameters):
Thresholds change progressively as a function of session, following an exponential learning curve with three parameters: the asymptote α, the magnitude of learning μ (i.e., $\mu = \theta_1 - \alpha$), and the learning rate τ. Learning proceeds in the transfer phase with no transfer costs:

$$\theta_i = \alpha + \mu e^{-\tau(i-1)} \qquad i \in I_{Train} \cup I_{Trans} \tag{2}$$

(II) Learning and arbitrary transfer costs (6 parameters):
Thresholds change progressively across the Training sessions, as in Model I. Thresholds in the Transfer sessions are modeled as arbitrary deviations from that learning curve (η_6, η_7, η_8):

$$\theta_i = \alpha + \mu e^{-\tau(i-1)} \qquad i \in I_{Train}$$
$$\theta_i = \alpha + \mu e^{-\tau(i-1)} + \eta_i \qquad i \in I_{Trans} \tag{3}$$

Finally, we compared these two models for each individual data set, following a likelihood ratio test described by Kingdom and Prins (2016), and accepted the fuller *Model II* if its likelihood was higher than that of the lesser *Model I* in more than 95% of 1000 bootstrap samples. As the lesser model corresponds to a special case of the fuller model, in which three of its parameters are set to zero, the likelihood-ratio test determines if the data are equally likely when these restrictions on the fuller model are made. Thus, using this conservative strategy, we accepted the more complex model only if it appeared necessary to explain the data.

A summary of each individual's data and model fits is shown in the Supplementary Material. Based on the model fits, we excluded 7 observers from our analyses who did not reach a contrast threshold of 100% or less during and beyond the second Training session (i.e., if any $\theta_{2-5} > 0$ in log units; see *# Poor performance* in Table 1) and 7 observers whose transfer costs were extraordinarily high (exceeding the factor ± 2 of the magnitude of learning; see *# Extreme transfer costs* in Table 1). One observer met both of these exclusion criteria. For all of the observers with extreme transfer costs, these costs had positive signs (i.e., performance was much poorer than expected). They are likely to indicate idiosyncratic asymmetries in visual performance across the

visual field) that violate the assumption of our experimental protocol that performance in all tested stimulus locations was comparable before training, which we made based on previous studies (e.g., Abrams, Nizam, & Carrasco, 2012; Carrasco, Talgar, & Cameron, 2001). Indeed, for these observers, our Temporal setback index of transfer costs (see next section) could not have been reliably estimated. Whereas we consider this exclusion criterion imperative here, we also recomputed all analyses reported in the results section when applying the poor-performance criterion only (resulting in N = 43) and found that only two of the significance statements reported in the results section would change; both do not challenge the conclusions of the manuscript. We added footnotes in the corresponding places.

2.7. Data analyses: indexes of transfer costs

We specifically designed our experiments to induce strong transfer costs when—after 5 days of training—observers switched from a Trained location and orientation of the DT to a new location and/or orientation (cf. Jeter et al., 2009). To estimate the changes in performance from the Training to the Transfer phase of each experiment, we used the parameter estimates of Model II to compute two indexes of transfer costs: Relative cost and Temporal setback (Fig. 2)—provided Model II accounted better for an individual's data than Model I (otherwise, the transfer cost indices described here were set to zero).

The Relative cost C (Fig. 2a) expresses the increase in contrast threshold in a given transfer session (i.e., parameters η_6, η_7, and η_8, as estimated in *Model II*) relative to the amount of learning that would have taken place at that point in time (based on an extrapolation of the learning curve). For each transfer session i, It can be computed from the estimated model parameters:

$$C = \frac{\eta_i}{\mu(1 - e^{-\tau(i-1)})}. \tag{4}$$

Here, the denominator is simply the amount of learning that would have occurred if training had continued from the Training to the Transfer phase. Therefore, this index assumes the value $C = 1$ if an observer's threshold is back at the level of the first day of the Training phase (i.e., η_i would have the same value as the denominator). In turn, if the numerator is 0, then $C = 0$. That is, there would be no deviations from the prediction based on the learning curve.

The Temporal setback parameter S (Fig. 2b), in turn, describes the number of sessions by which the observer's performance has been set back in a given transfer session. Using the inverse of the learning curve (which expresses session as a function of threshold), it can be computed as:

$$S = i - 1 - \frac{\ln\left(\frac{(\theta_i - \alpha)}{\mu}\right)}{-\tau} \tag{5}$$
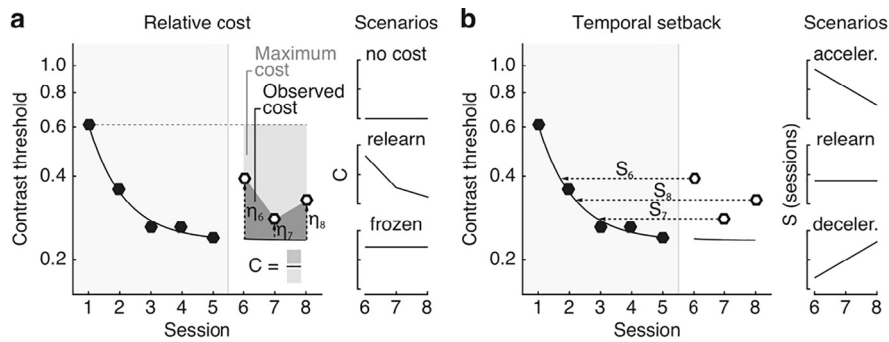
Fig. 2. Measures of transfer cost and scenarios for possible outcomes. a Relative cost C, which expresses the transfer cost in a given transfer session (η_6, η_7 and η_8) relative to the amount of learning that would have occurred if training had continued (i.e., the difference between the prediction based on the learning curve and the threshold in Training session 1). Possible scenarios include no transfer costs (top), relearning (middle), and frozen costs with no improvement across transfer sessions (bottom) b Temporal setback S, which expresses the number of sessions an observer has lost due to the transition to the Transfer phase (i.e., by how many sessions performance was set back). Scenarios include an accelerated relearning (top), a relearning at the same rate as during the Training phase (middle), and a decelerated relearning (bottom). Note that if no transfer costs are observed in a given session (i.e., $C_i = 0$), then S_i would be 0 as well.

As an example, if in the first session of the Transfer phase, an observer's threshold returns to the level of the first day of the Training phase, the setback would be 5 sessions (as there were 5 sessions of training). This can be understood considering the equation above: On the first day of the Training phase, the threshold is defined as $\theta_1 = \mu + \alpha$. Therefore, $\theta_1 - \alpha = \mu$, such that the logarithmic term becomes zero, and S becomes $i-1$ (i.e., 5 sessions for session 6). On the other hand, if no cost is observed in a given transfer session (e.g., $\eta_6 = 0$), then the term involving the logarithm assumes the value $i-1$, such that S becomes zero. For the rare cases that $\theta_i < \alpha$ (i.e., the threshold is below the asymptote of learning), the log is undefined as there is no point in time at which that level of performance had been reached; in these cases, we set S to 0.

Note that the two parameters illuminate different aspects of the transfer costs. Whereas the Relative cost C provides an index of the magnitude of transfer costs in terms of threshold increase, the Setback parameter S emphasizes the temporal domain of the learning process, giving insight into acceleration or deceleration of re-learning in the transfer phase (see Scenarios in Fig. 2b).

3. Results

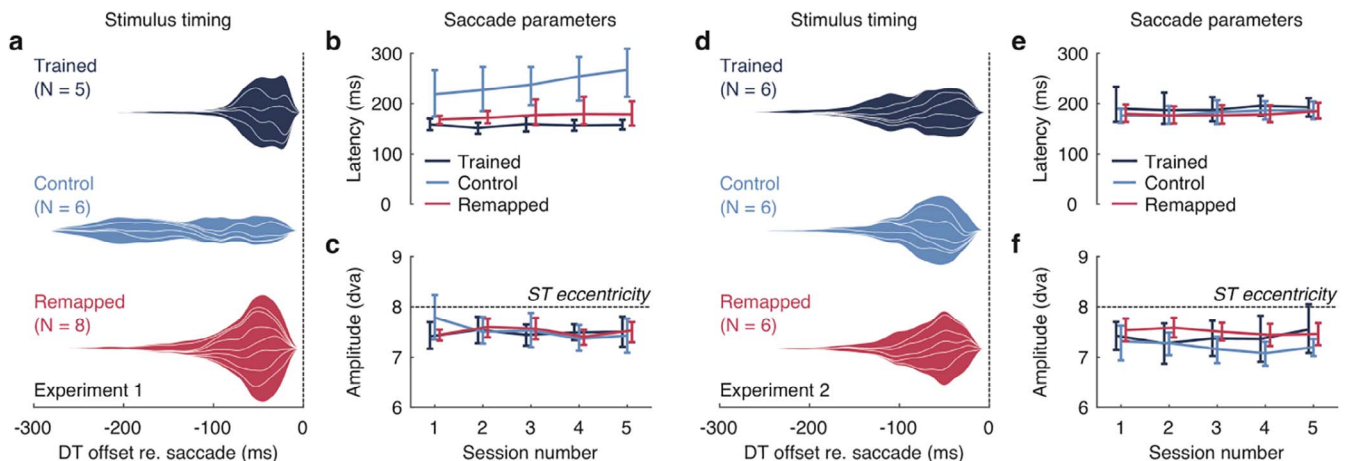### 3.1. Stimulus timing

We monitored saccade onset and landing sites online (see Section 2), to ensure that the DT (oriented Gabor) had been removed from the screen as soon as the eyes left the fixation area. To confirm the reliability of this procedure, we determined the timing of the DT relative to

the onset of saccades detected offline for all training trials (transfer trials did not contain saccades). Across all observers and conditions, the average median delay between DT offset and saccade onset was 80.9 ms in Experiment 1 and 73.1 ms in Experiment 2. With the exception of the Control group in Experiment 1, the distributions of DT offsets were tightly locked to the saccade (see Fig. 3a,d): in the majority of trials, the DT disappeared within 100 ms of saccade onset. As the interval between ST and DT onset was fixed, the deviation of the Control group in Experiment 1 (Fig. 3a) was a direct consequence of larger inter-individual variability in saccade latencies in that group, which was not apparent in the other conditions (see below). Importantly, across both experiments, there was no single trial in which the DT disappeared after saccade onset, ensuring that—in the Training phase—the DT only ever stimulated one location on the retina. Consequently, the remapped location (i.e., the location the stimulus would have on the retina after the saccade) was never physically exposed to the training stimulus.

3.2. Saccade parameters

Saccades had a median latency of 191 and 184 ms on average (Experiment 1 and 2, respectively), and a median amplitude of 7.50 and 7.37 dva, somewhat undershooting the target eccentricity of 8 dva (as typically found, e.g., Becker, 1989). To explore any possible differences in these saccade parameters across conditions, we conducted mixed-model analyses of variance (ANOVA) with the between-subject factors Transfer location (trained vs control vs remapped) and Saccade direction (downward vs rightward), and the within-subject factor Session (1

Fig. 3. Stimulus timing and saccade parameters for Experiments 1 (a–c) and Experiment 2 (d–f). a,d Violin plots of DT offset relative to saccade onset for experimental condition. The silhouette represents the overall distribution; each stripe corresponds to one participant. b,e Average median saccade latency as a function of condition and session number. c,f Average median saccade amplitude as a function of condition and session number. Saccades landed slightly short of the ST, which had an eccentricity of 8 dva. Error bars are bootstrapped $CI_{95\%}$.
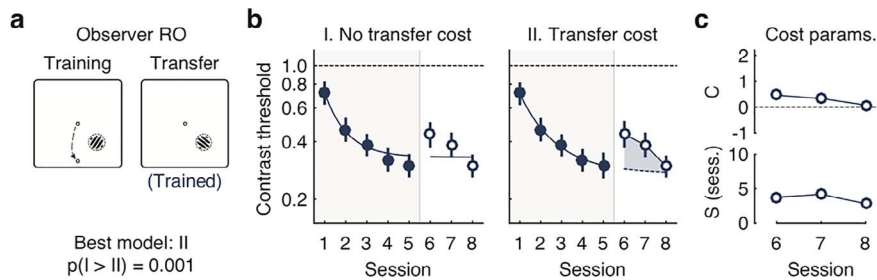
Fig. 4. Individual data and model fits for one observer (RO). a Stimulus layout in the Training and Transfer phase of Experiment 1. For this observer, saccade direction was downward and transfer was tested at the Trained location. b Contrast threshold estimates based on model fits. Data points show thresholds from fits of psychometric functions to each session's data, using slope and lapse rates estimated from all training sessions, along with bootstrapped $CI_{95\%}$. Solid lines show model fits with the additional assumption that all sessions—in the Training and the Transfer phase—are described by a single learning curve (Model I: No transfer cost), or that a learning curve describes performance changes during the Training phase whereas thresholds can deviate arbitrarily from that curve in the Transfer phase (Model II: Transfer cost). Model II provided the best fit for this observer. c Transfer cost indexes, Relative cost C and Temporal setback S, estimated based on parameters of Model II. See Section 2 for details and Supplementary Information for all individual data.

through 5), for each experiment. Note that with the exception of the influence of Saccade direction, any impact of conditions on saccade parameters must—by definition—result from incidental inter-individual differences, as all conditions across the two experiments had identical training phases. Being aware of these differences is important, however, as they may entail consequences for the evolution of perceptual learning, as well as its spatial and feature specificity.

In Experiment 1, saccade latencies differed as a function of transfer location ($F(2,13) = 6.34$, $p = .012$), due to longer latencies in the group assigned to the Control location (Mean = 241 ms; see Fig. 3b) than the other locations (Trained: 157 ms; Remapped: 175 ms). Saccade direction and session did not influence saccade latencies, nor were there any interactions among the three factors (all Fs < 1.62, ps > 0.16). Saccade amplitudes were homogeneous across all groups and sessions (all Fs < 1; Fig. 3c).

In Experiment 2, saccade latencies did not vary as a function of transfer location, saccade direction, or session, and no significant interactions were observed (all $Fs < 1.42$, $ps > 0.24$; Fig. 3e). However, saccade amplitude varied as a function of saccade-direction ($F(1,13) = 11.2$, $p = .006$), with slightly shorter saccades in the downward (7.12 dva) than in the rightward group (7.57 dva). No other factors influenced saccade amplitude (all Fs < 1.77, ps > 0.15; Fig. 3f).

3.3. Changes in visual performance across time

By relating each observer's perceptual reports (clockwise or counterclockwise with respect to the reference orientation) to stimulus contrasts, and fitting psychometric functions to the data of each session, we determined (1) the evolution of contrast thresholds across days of training and (2) the costs associated with transfer to a different location and stimulus orientation (Fig. 4; see Section 2 for details). More specifically, we proceeded in three steps: First, for each individual, we compared two alternative models of how contrast thresholds may have evolved over sessions: (I) a simple learning model assuming an exponential change of the individual's contrast threshold that continues throughout the Training and the Transfer phase, and (II) the same simple learning model, but with a significant change in threshold after the transition to the Transfer phase (Fig. 4b). Second, for each experiment, we evaluated the learning that occurred in each experimental group, that is, as a function of Transfer location and Saccade direction. Third, we compared the transfer costs that we observed as a function of the transfer condition.

3.3.1. Model selection

For 13 out of 19 participants in Experiment 1, and 13 out of 18 participants in Experiment 2, Model II, which included transfer costs in addition to a continuous change of the individual's contrast threshold throughout the Training phase, provided a better fit of the data (see Supplementary Information for individual fits). Indeed, transfer cost

parameters were required for the majority of participants in each but one condition (Fig. 5a). The exception occurred for the group tested at the Trained location in Experiment 2: When neither the stimulus location nor its orientation changed from the Training to the Transfer phase, significant transfer costs occurred in only 1 out of 6 participants (Fig. 5a).

In the following sections, we assess learning parameters as well as indexes of transfer cost, based on whichever model best accounts for each individual's data. That is, if Model I (No transfer cost) has been selected for a given participant, learning parameters are those obtained from the fit of Model I, and transfer cost indices C and S are both defined as zero. In contrast, if Model II (Transfer cost) has been selected for a given participant, learning parameters are those obtained from the fit of Model II, and transfer cost indices C and S are derived according to Eqs. (4) and (5), respectively (see Section 2).

3.3.2. Pre-saccadic training increases contrast sensitivity

For each participant, we obtained the three parameters of the learning curve describing threshold changes in the Training phase (Model II) or across the entire experiment (Model I): the asymptote α, the magnitude of learning μ, and the learning rate τ. Across the two experiments, the different experimental groups underwent the exact same training procedure in each condition (except for saccade direction). Therefore, any differences of these parameters as a function of Transfer location are incidental, but must be known in order to interpret differences in transfer costs across conditions. To address violations of normality and heteroscedasticity of the data (see violin plots in Fig. 5b–d), we used non-parametric tests to assess differences between conditions.

In Experiment 1, the magnitude of learning had a median of 0.322 units of log contrast, which was significantly different from zero (signed-rank test, $p < .001$). A Wilcoxon rank-sum test showed that Saccade direction did not elicit a statistically significant difference in the Magnitude of learning ($Z = 109$, $p = .497$). Further, a Kruskall-Wallis ANOVA yielded no evidence for Magnitude differences as a function of Transfer location ($\chi^2(2) = 2.264$, $p = .322$; Fig. 5b). Similarly, the asymptote of learning did not vary significantly with Saccade direction ($Z = 84$, $p = .211$) or Transfer location ($\chi^2(2) = 0.984$, $p = .611$; Fig. 5c); across conditions, it had a median of -0.354 log contrast (or, 44.2%). Finally, the rate of learning had a median of 0.979 session^{-1}. Again, it did not vary significantly with Saccade direction ($Z = 101$, $p = .968$) or Transfer location ($\chi^2(2) = 0.783$, $p = .676$; Fig. 5d).

In Experiment 2, the results were very similar. The magnitude of learning had a median of 0.356 log units that was significantly different from zero (signed-rank test, $p < .001$). Saccade direction did not elicit a statistically significant difference in the Magnitude of learning ($Z = 82$, $p = .633$), and there was no evidence for Magnitude
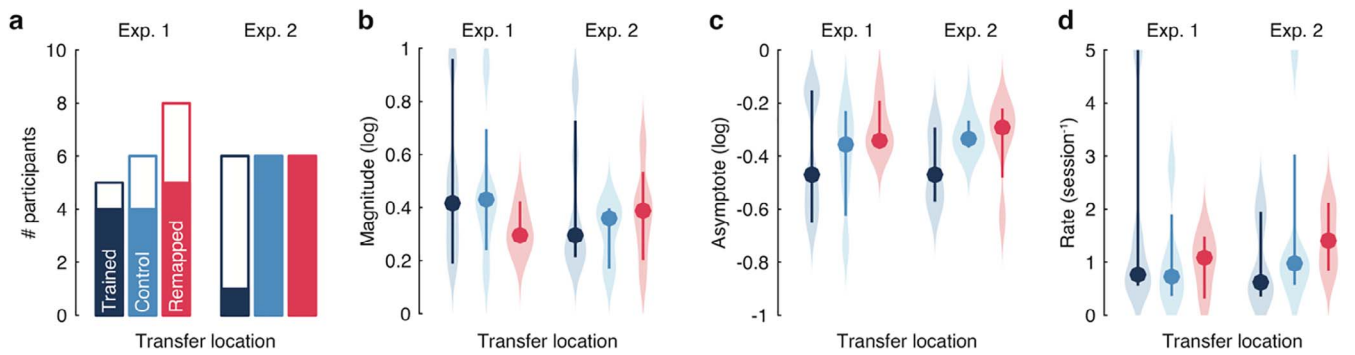
Fig. 5. Prevailing model and learning parameters for Experiments 1 and 2 as a function of Transfer location. a Number of participants for which Model I (white) or Model II (colored) prevailed in model selection. b–d Learning parameters. Magnitude (b), Asymptote (c), and Rate (d) of learning as estimated for the prevailing model. Violin plots show distribution of parameter across participants; dots show the median and error bars represent its bootstrapped CI$_{95\%}$.

differences as a function of Transfer location ($\chi^2(2) = 0.573$, $p = .751$; Fig. 5b). The asymptote of learning also did not vary significantly with Saccade direction ($Z = 77$, $p = .965$) or Transfer location ($\chi^2(2) = 2.538$, $p = .281$; Fig. 5c); across conditions, it had a median of -0.329 log contrast (or, 46.9%). Finally, the rate of learning had a median of 0.967 log units per session. Again, it did not vary significantly with Saccade direction ($Z = 77$, $p = .965$) or Transfer location ($\chi^2(2) = 2.140$, $p = .343$; Fig. 5d).

Thus, we found clear evidence that training with stimuli presented just prior to saccadic eye movements results in a significant increase in contrast sensitivity over time. Magnitude, Asymptote, and Rate of

Fig. 6. Transfer cost parameters for Experiments 1 and 2 as a function of Transfer location, averaged across sessions (a,b) and as a function of session (c,d). a Relative cost quantifies the transfer cost in a given Transfer session relative to the learning predicted based on the extrapolation of the learning observed in the Training phase. Violin plots show distribution of the parameter across participants; dots show the median and error bars represent its bootstrapped CI$_{95\%}$. A Relative cost of 0 indexes perfect transfer (i.e., learning continued as predicted by the learning curve); a value of 1 indexes that thresholds in the Transfer phase returned to the level observed in the first Training session. b Temporal setback quantifies the number of sessions of training lost after entering the Transfer phase. c Evolution of median Relative cost across sessions. d Changes in Temporal setback across sessions. Error bands represent the bootstrapped CI$_{95\%}$ of the median.

learning were of similar magnitude in the two experiments. Although these learning parameters did not vary significantly across experimental groups, they did vary substantially across individuals. We, therefore, express transfer cost indexes relative to the learning curve of each individual—a key feature of both measures of transfer costs reported below.
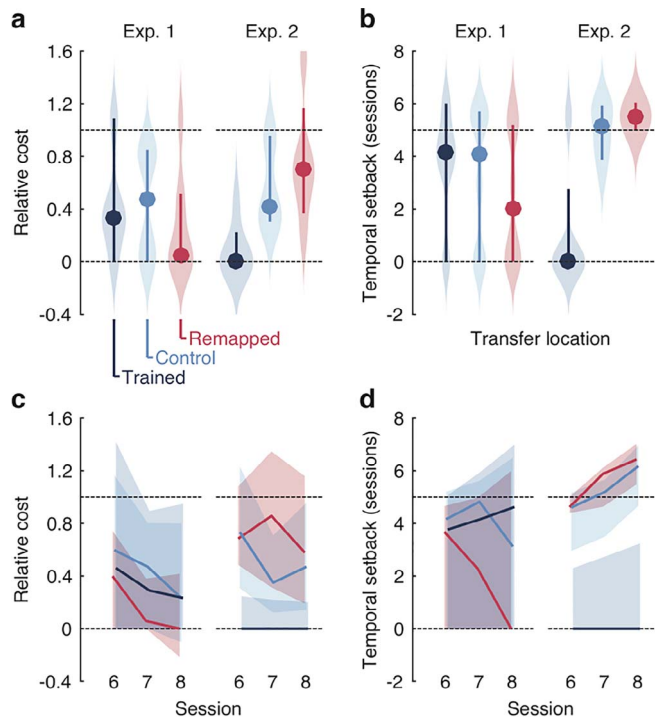
3.3.3. Transfer costs after changes in location or orientation

For a large majority of participants, model selection provided evidence for significant deviations from the learning curve after changes in location and/or orientation of the DT (see Fig. 5a). To determine the nature and magnitude of transfer costs for each observer, we calculated two indices of transfer costs (Fig. 2). In a first step, we determined the average of each of these indices across the three Transfer sessions to assess general patterns across experimental conditions.

First, we calculated a measure of the *Relative cost* (Fig. 2a), which assumes the value 0 if transfer were perfect (i.e., learning continued as predicted by the learning curve), and 1 if thresholds in the Transfer phase returned to the level observed in the first Training session. In Experiment 1, Relative costs had a median of 0.292 across all participants, which was significantly different from both 0 and 1 (signed-rank test, $ps < 0.001$). Although the median Relative cost was considerably smaller at the Remapped location than at the Trained or the Control location, participants varied strongly with respect to this index (Fig. 6a), and a Kruskall-Wallis ANOVA yielded no evidence for differences as a function of Transfer location ($\chi^2(2) = 0.811$, $p = .667$). Moreover, Saccade direction did not elicit a statistically significant difference in this measure ($Z = 117$, $p = .170$).

In Experiment 2, the Relative costs had a median of 0.388 across all participants, which was significantly different from both 0 ($p < .001$) and 1 ($p = .001$). In contrast to Experiment 1, costs differed across Transfer locations ($\chi^2(2) = 9.470$, $p = .009$). Whereas the Relative cost was indistinguishable from 0 at the Trained location ($p = 1.000$), significant costs were observed for the Remapped and for the Control location ($ps < 0.05$; Fig. 6a). Moreover, at the Trained location, the Relative cost was significantly lower than at the Remapped ($Z = 54$, $p = .004$) or the Control locations ($Z = 54$, $p = .009$). Saccade direction did not elicit a statistically significant difference in this measure ($Z = 78$, $p = .895$).

Second, we calculated the *Temporal setback* (Fig. 2b), which provides an estimate of how many sessions ago performance was at the same level as observed in the transfer phase. Thus, this parameter assumes the value 0 sessions if no costs were observed and the value 5 sessions if participants had to restart learning from their level of performance in session 1. In Experiment 1, Temporal setback had a median of 3.57 sessions across all participants, which was significantly different from both 0 (i.e., no transfer costs; $p < .001$) and 5 (i.e., a complete

setback to the level of performance in the first session; $p = .014$[1]. As for the Relative cost reported above, the median Temporal setback was numerically smaller at the Remapped location than at the Trained or the Control location (Fig. 6b), but a Kruskall-Wallis ANOVA yielded no evidence for differences as a function of Transfer location ($\chi^2(2) = 0.562$, $p = .755$). Temporal setback did not vary significantly across Saccade directions ($Z = 121$, $p = .095$).

In Experiment 2, the Temporal setback had a median of 4.98 sessions across all participants, which was significantly different from 0 ($p < .001$), but indistinguishable from 5 ($p = .371$). Temporal setback varied significantly with Transfer locations ($\chi^2(2) = 8.221$, $p = .016$); significant Temporal setback was observed for the Remapped and for the Control location ($ps < 0.05$; Fig. 6b), where it could not be distinguished from 5 sessions ($ps > 0.15$). At the Trained location, Temporal setback could not be distinguished from 0 ($p = .250$) and was significantly lower than for the two other Transfer locations ($Zs = 54$, $ps = 0.015$). Saccade direction did not elicit a statistically significant difference in this measure ($Z = 78$, $p = .895$).

Altogether, we find that perceptual learning for stimuli presented before saccades is strongly selective to both the trained location and orientation. Across both experiments, transfer costs were comparable at the remapped and the control location, as well as at the trained location if the orientation changed in the transfer phase. Relative costs averaged to about 30–40% of the observed learning, which corresponded to about 3.5 to 5 sessions of Temporal setback. Transfer costs did not occur if transfer was tested for the Trained stimulus orientation (Experiment 2) at the Trained location, despite the change in the instructed eye movement behavior between the Training and the Transfer phase.

3.4. Evolution of performance in the transfer phase

As we tested performance in a total of three Transfer sessions, we were able to investigate the pattern of relearning after experienced transfer costs (see scenarios in Fig. 2). Fig. 4c shows an example of one observer's evolution of Relative cost and Temporal setback across Transfer sessions (see Supplementary Information for all observers).

In Experiment 1, we observed a pattern of relearning after the transition to a new stimulus orientation and/or location: The Relative cost decreased over the course of the transfer sessions (Fig. 6c) while the Temporal setback stayed more or less constant (Fig. 6d). Indeed, a non-parametric Friedman's test suggested a significant effect of Session on the Relative cost for the Remapped ($\chi^2(2) = 7.600$, $p = .022$) and for the Trained location ($\chi^2(2) = 6.000$, $p = .050$); this effect did not reach significance for the Control location ($\chi^2(2) = 2.000$, $p = .368$)[2]. Temporal setback did not change as a function of Session for any of the Transfer locations (all χ^2s(2) < 3.2, $ps > 0.200$).

In Experiment 2, we did not see evidence of relearning. Instead, Relative costs at the Remapped and at the Control location remained largely constant across the Transfer sessions (Fig. 6c; all χ^2s(2) < 4.34, $ps > 0.115$). Indeed, the Transfer costs appeared to be frozen, resulting in a systematic increase in the Temporal setback parameter over transfer sessions (Fig. 6d; Control: $\chi^2(2) = 10.333$, $p = .006$; Remapped: $\chi^2(2) = 8.333$, $p = .016$).

Together, these results suggest that relearning occurred after a change in the stimulus orientation (Experiment 1). In contrast, if the stimulus merely changed its location, but not its orientation (Experiment 2), the Transfer costs remained high even after three Transfer sessions.

---

[1] When we included all observers with extreme transfer costs in the analysis (see Section 2), the Temporal setback in Experiment 1 is no longer distinguishable from 5 ($p = .110$).
[2] When we included all observers with extreme transfer costs in the analysis (see Section 2), the effect of Session on the Relative cost becomes significant also for the Control location of Experiment 1 ($p = .028$).

4. Discussion

We assessed perceptual learning of stimuli presented just before saccadic eye movements, during motor preparation. The target stimulus was a briefly flashed, oriented Gabor (embedded in noise) that appeared at a single location in the visual periphery while observers prepared a saccade to a different, predefined location. We adjusted the contrast of this stimulus on every trial to determine the observer's sensitivity to the stimulus across sessions. Using this protocol, we pursued three main objectives: First, we assessed if perceptual learning proceeds if stimuli are presented strictly during saccade preparation. Second, we determined the specificity of this pre-saccadic learning process to the trained location and feature. Finally, we investigated if learning transferred to the location the pre-saccadic stimulus would have after the eye movement—the remapped location. In the following, we first discuss the two complementary measures we used to assess perceptual learning and then our results in relation to each of the three objectives.

4.1. Complementary measures to assess perceptual learning and re-learning

We developed two measures of transfer costs that can be calculated based on learning curves fitted to performance changes in the Training phase. These two measures take into account individual differences in learning and reflect changes in performance during the Transfer phase in complementary ways (Fig. 2). The first measure, Relative cost, is comparable to previous measures of transfer costs (or, specificity indexes), which often express the decrement in performance in the Transfer phase relative to the improvement obtained by the end of the Training phase (e.g., Ahissar & Hochstein, 1997; Donovan et al., 2015; Dosher, Han, & Lu, 2010; Jeter et al., 2009; Petrov & Hayes, 2010). In contrast to these previous indexes, however, Relative cost also considers the expected progress of learning that would have occurred had training continued further (i.e., had a transfer session been an additional training session). Our result that thresholds in the Transfer phase were indeed indistinguishable from the predictions of the learning curve when the stimulus location and orientation remained unchanged validates this procedure.

The second measure, Temporal setback, expresses the loss of learning suffered from entering the Transfer phase in terms of time, instead of perceptual sensitivity. Indeed, the Temporal setback would show an increase across Transfer sessions if performance remained constant during the Transfer phase, providing statistically quantifiable evidence of the absence of relearning. Similarly, a constant setback would result in a continuous change of the Relative cost across Transfer sessions. We propose using these two measures in future studies of perceptual learning, to provide stronger evidence for the presence or absence of relearning, and to gain a better understanding of the learning mechanisms involved.

4.2. Perceptual learning before saccades

We found unequivocal evidence for learning. Contrast thresholds decreased continuously throughout the Training phase and could be modeled as an exponential, decelerating learning curve. The magnitude of this improvement differed across individuals, but was substantial on average, reaching about 0.35 units of log contrast below its starting value after five days of training. This improvement in sensitivity is comparable to that observed in a very similar task during fixation (Jeter et al., 2009). This result provides evidence for learning from pre-saccadic stimuli, demonstrating that the feature of the stimulus was efficiently processed by the visual system. This is remarkable as our own research and that of others has shown time and again that attention shifts to the target of an imminent saccade in an obligatory fashion and that this pre-saccadic attention shift is spatially selective to the saccade target (Baldauf & Deubel, 2008; Deubel & Schneider, 1996; Hoffman &

Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Montagnini & Castet, 2007; Ohl et al., 2017; A. L. White, Rolfs, & Carrasco, 2013). Clearly, the task was taxing for observers: They performed a fine orientation-discrimination task on a noisy stimulus that was briefly flashed in the visual periphery while they planned a saccadic eye movement to a different location. These challenges were reflected in the fact that a number of observers did not pass our performance criteria (see Section 2). Those observers who reached an acceptable performance level may have been able to more aptly allocate their resources to complete both the oculomotor and the perceptual task in a short time period.

As the discrimination target was the relevant stimulus for the perceptual task, and thus needed to be attended, learning could reflect observers' ability to allocate attention away from the saccade target. That it is possible, in principle, to attend to non-target locations has been shown in a range of different situations (Born, Ansorge, & Kerzel, 2013; Jonikaitis & Theeuwes, 2013; Montagnini & Castet, 2007; A. L. White et al., 2013), although it is often associated with impoverished saccadic performance (Deubel, 2008; Hoffman & Subramaniam, 1995; Kowler et al., 1995). Moreover, other studies using exogenous cues to draw attention to locations other than an imminent saccade target have provided evidence for an allocation of attention to the cued location (Jonikaitis et al., 2013; Szinte et al., 2016). Thus, learning to attend to the stimulus location may have played a role in the current task. Were this the only learning process, however, we would have not expected transfer costs at the trained location when the orientation of the stimulus changed.

4.3. Spatial and feature specificity of learning

Using the two parameters of transfer costs discussed above, we found clear evidence of specificity of learning to the trained location and feature. If the location and feature remained the same throughout the entire experiment, learning smoothly proceeded throughout the transfer phase with no evidence for costs when merely switching from a pre-saccadic presentation (in the Training phase) to a presentation during fixation (in the Transfer phase). Transfer costs were clearly evident, however, when either location or orientation of the stimulus changed from the Training to the Transfer phase. The observed feature specificity is a clear signature of perceptual learning and suggests that participants' performance reflects a change in the stimulus representation, not merely improved deployment of attention to the stimulus location while preparing a saccade.

The magnitude of the observed transfer costs was substantial, often setting performance back to the level observed on the first day of training. Moreover, transfer costs of changes in location and orientation were not explained by independent effects of feature and location specificity and thus not simply additive. Finally, if transfer costs were observed, sensitivity could improve once more. However, this second learning process during the Transfer phase was manifest only after a feature change (Experiment 1), and it was slowed down as compared to the speed of learning observed during the initial training.

In recent years, some protocols have been shown to overcome specificity and to facilitate transfer of location and feature learning. For instance, the "double training" protocol has shown location transfer and feature transfer. This protocol requires participants to perform a second task with stimuli presented at the untrained retinal locations throughout training (Hung & Seitz, 2014; Wang et al., 2014; Wang, Zhang, Klein, Levi, & Yu, 2012; Xiao et al., 2008) or at some time before a post-test (Zhang, Cong, et al., 2013; T. Zhang, Xiao, Klein, Levi, & Yu, 2010). Moreover, without additional training either at the untrained locations and with minimum effort from the observer, the exogenous-covert-attention training protocol has shown that training with exogenous attention enables perceptual learning (Szpiro & Carrasco, 2015) and facilitates location transfer across the same and different hemifields (Donovan et al., 2015), even when observers are tested under neutral

conditions. Based on these findings, and on the similarity of the perceptual consequence of pre-saccadic attention and covert attention (e.g., Rolfs & Carrasco, 2012) and covert attention (Carrasco, Ling, & Read, 2004; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010), it seemed possible that transfer would have occurred to other attended locations in our protocol. On the other hand, based on differences between pre-saccadic (e.g., Li et al., 2016) and covert attention (e.g., Ling, Liu, & Carrasco, 2009; Talgar, Pelli, & Carrasco, 2004), it was also possible that transfer would not necessarily occur at other attended locations.

4.4. No evidence for transfer of learning to the remapped location

The fact that the observed learning from pre-saccadic stimuli was specific to both the trained location and orientation allowed us to address an additional intriguing question: In comparison to the control location, do we observe reduced transfer costs at the remapped location—that is, the location the pre-saccadic stimulus would have had after saccade landing? And if so, is this transfer specific to the trained feature or a purely spatial phenomenon?

We did not observe consistent facilitation due to pre-saccadic remapping. In Experiment 1, many observers showed little or no evidence for transfer costs at the remapped location. Indeed, based on preliminary analyses, we had reported some transfer to the remapped location in oral presentations (Rolfs, Murray-Smith, & Carrasco, 2012, 2013). However, variability across participants was substantial, and using the rigorous psychophysical modeling approach advanced here, these effects were found to be unreliable. More critically, in Experiment 2, transfer costs were substantial at the remapped locations.

Given the substantial evidence for the impact of predictive remapping on different aspects of perceptual function (Harrison et al., 2013; He et al., 2017; Hunt & Cavanagh, 2011; Jonikaitis et al., 2013; Puntiroli et al., 2015; Rolfs et al., 2011; Szinte et al., 2015, 2016), why did we not observe facilitation at the remapped location? Several points seem to play a role. First, our dependent variable (contrast sensitivity) may not have been sensitive enough to capture the consequences of remapping for learning: transfer costs in our protocol were often very large, and may have overshadowed modulatory effects.

Second, our protocol was different from most behavioral studies of predictive remapping in that the pre-saccadic stimulus never had a post-saccadic counterpart. This was, of course, done on purpose, as we took great care to avoid any visual stimulation at the remapped location that could have induced learning (or, transfer of learning) over time. It is likely that remapping is a process that is calibrated from trial to trial, based on post-saccadic visual feedback, much like our eye movements are continuously adjusted to match their visual goals (Cassanello, Ohl, & Rolfs, 2016; Collins, Rolfs, Deubel, & Cavanagh, 2009). If throughout many trials and days of training, no such feedback is ever provided, the visual system might no longer bother predicting a post-saccadic stimulus when it is only ever present before a saccade—remapping would be unlearned in this context. Unfortunately, we cannot address this hypothesis using the current data, as we did not manipulate or track this possible unlearning across time. This hypothesis could be investigated using a broad range of protocols that can assess remapping (see Thakkar, Diwadkar, & Rolfs, 2017 for an overview).

Third, an alternative yet related hypothesis is that training enables the visual system to engage attention at the discrimination target location at just the right time, and to disengage subsequently. In that scenario of temporal attentional selection (e.g., Coull & Nobre, 1998; Denison, Heeger, & Carrasco, 2017), the attended item could be unattended by the time the remapping takes place.

Finally, and perhaps most importantly, it is possible that the processes that follow from predictive remapping are not the same as those that drive perceptual learning. Pre-saccadic remapping predictively updates attention, from relevant locations to their future retinotopic locations before the onset of eye movements (Rolfs et al., 2011), and

this effect has been shown for voluntarily as well as involuntarily attended locations (Jonikaitis et al., 2013; Szinte et al., 2015, 2016). There is evidence that exogenous covert attentional cues, presented prior and adjacent to the target during training while observers fixate, can enable perceptual learning (Szpiro & Carrasco, 2015) and induce transfer of learning to the untrained locations (Donovan et al., 2015). Note that these studies feature both an exogenous cue and a resulting attention shift. The present study, arguably, featured the latter: Evidence from neurophysiology and psychophysics is now converging that attention needs to be allocated to a location before its remapping can take effect (Rolfs & Szinte, 2016); given the predictability of the location and timing of the stimulus in the current task (the discrimination target was displayed 80 ms after the onset of the saccade target, and always at the bottom left of fixation), this precondition was likely met. We conjecture, therefore, that pre-saccadic attentional allocation to a location that is never exposed to a stimulus is not sufficient to induce perceptual learning and learning transfer in the way that exogenous attention does. Future studies that provide an irrelevant visual stimulus at the untrained locations upon saccade landing, and which potentially manipulate the time between an attentional cue and the task-relevant discrimination target (as in Jonikaitis et al., 2013; Szinte et al., 2016), may have a better chance to probe perceptual learning at the remapped location. Beyond providing a test bed for the mechanisms of perceptual learning and remapping, establishing this link would test the hypothesis that perceptual learning in non-retinotopic reference frames (E. Zhang & Li, 2010) is enabled by predictive remapping of attention across saccades (E. Zhang, Zhang et al., 2013a).

4.5. Predictive remapping of stimulus features (in addition to locations) remains elusive

At the outset of this study, we advanced the idea that perceptual learning could be used to better understand pre-saccadic remapping: Does this mechanism work in a purely spatial domain, updating attention as the eyes move, or does it entail predictions about the features at these updated locations? The absence of a robust remapping effect in our data renders this dissociation impossible. Our study thus joins the ranks of previous psychophysical attempts that have yielded inconclusive results with respect to this question (see Section 1).

Finding robust evidence for feature remapping has been an impossible quest not just for psychophysical research; neuroimaging studies using functional magnetic resonance imaging (fMRI) have been suffering the same fate. Early fMRI studies of predictive remapping have provided consistent evidence for the spatial updating of stimulus-related signals in a wide range of visual cortical areas (Medendorp, Goltz, & Vilis, 2005; Medendorp, Goltz, Vilis, & Crawford, 2003; Merriam, Genovese, & Colby, 2003; Merriam, Genovese, & Colby, 2007). This predictive remapping signal contains information about the spatial profile of a stimulus, appropriately scaling the pattern of neural activation from a peripheral location (i.e., the saccade target) to the fovea (Knapen, Swisher, Tong, & Cavanagh, 2016). Whereas this intriguing result provides a possible neural correlate of trans-saccadic object-based attention, it does not reveal remapping of non-spatial visual features.

To address this question more directly, one study used multivariate pattern analysis to specifically decode feature information (faces vs. houses) from visual cortex, and found no evidence for predictive remapping of stimulus features in any visual area (Lescroart, Kanwisher, & Golomb, 2016). However, this study also failed to find any reliable signatures of remapping of stimulus location, a prerequisite of feature remapping. A more successful avenue of research has used fMRI adaptation in response to stimulus repetition to probe trans-saccadic feature updating (albeit not predictive remapping before a saccade): If a large, oriented grating is shown at the same location on the screen, before and after a saccade, then the blood-oxygen-level dependent (BOLD) signal in parietal and extrastriate areas is reduced in response

to a repeated orientation as compared to an orthogonal one (Dunkley, Baltaretu, & Crawford, 2016). Moreover, trans-saccadic fMRI adaptation—to a repeated stimulus of the *same* orientation—has been found to be spatially specific in frontal and parietal regions as well as in extrastriate and (to a lesser extent) striate cortex (Fairhall, Schwarzbach, Lingnau, Van Koningsbruggen, & Melcher, 2017). Whereas these results are compatible with spatial updating of feature information, the critical link—trans-saccadic fMRI adaptation that is both feature and spatially selective—is still missing. It appears possible, for instance, that feature information need not be updated, if it is independent of space across saccades (Kalogeropoulou & Rolfs, 2017).

All of these studies are compatible with the idea that remapping is generally limited to spatial pointers to attended targets (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Rolfs & Szinte, 2016) or, alternatively, objects (Melcher & Colby, 2008), although the latter would indeed predict predictive remapping of feature information. Positive evidence for predictive remapping of feature information could distinguish between these ideas. Thus far, such evidence remains elusive.

5. Conclusion

Probing observers' performance in a challenging perceptual task during saccade preparation, we have shown that spatial and feature specificity—two key features of visual perceptual learning—subsist even if training is constrained to periods of saccade preparation. Despite the absence of traces of remapping in our perceptual learning protocol, we document the first data ever collected in this regard. Crucially, we developed and employed a range of methods in this study, including the comparative modeling of entire data sets and the calculation of complementary model-based transfer indices that are sensitive and meaningful while taking into account individual learning parameters. These methods may provide a novel framework for continuing research on perceptual learning and its underlying processes. We hope that future studies will further explore perceptual learning during active vision and other more naturalistic contexts.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2017.11.009.

References

Abrams, J., Nizam, A., & Carrasco, M. (2012). Isoeccentric locations are not equivalent: The extent of the vertical meridian asymmetry. *Vision Research, 52*(1), 70–78.

Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature, 387*(6631), 401–406. http://dx.doi.org/10.1038/387401a0.

Baldauf, D., & Deubel, H. (2008). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research, 184*(3), 411–425. http://dx.doi.org/10.1007/s00221-007-1114-x.

Ball, K., & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science, 218*(4573), 697–698. http://dx.doi.org/10.1126/science.7134968.

Becker, W. (1989). The neurobiology of saccadic eye movements. Metrics. *Reviews of Oculomotor Research, 3*, 13–67.

Biber, U., & Ilg, U. J. (2011). Visual stability and the motion aftereffect: A psychophysical study revealing spatial updating. *PLoS ONE, 6*(1), e16265. http://dx.doi.org/10.

1371/journal.pone.0016265.

Born, S., Ansorge, U., & Kerzel, D. (2013). Predictability of spatial and non-spatial target properties improves perception in the pre-saccadic interval. *Vision Research, 91*, 93–101. http://dx.doi.org/10.1016/j.visres.2013.08.003.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*(4), 433–436.

Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature, 371*(6497), 511–513. http://dx.doi.org/10.1038/371511a0.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience, 7*(3), 308–313. http://dx.doi.org/10.1038/nn1194.

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: Effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spatial Vision, 15*(1), 61–75.

Cassanello, C. R., Ohl, S., & Rolfs, M. (2016). Saccadic adaptation to a systematically varying disturbance. *Journal of Neurophysiology, 116*, 336–350.

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on re-mapping of attention pointers. *Trends in Cognitive Sciences, 14*(4), 147–153. http://dx.doi.org/10.1016/j.tics.2010.01.007.

Cavanaugh, M. R., Zhang, R., Melnick, M. D., Das, A., Roberts, M., Tadin, D., ... Huxlin, K. R. (2015). Visual recovery in cortical blindness is limited by high internal noise. *Journal of Vision, 15*(10), 1–18.

Collins, T., Rolfs, M., Deubel, H., & Cavanagh, P. (2009). Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *Journal of Vision, 9*(5), 1–9. http://dx.doi.org/10.1167/9.5.29.

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers: a Journal of the Psychonomic Society Inc, 34*(4), 613–617.

Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *The Journal of Neuroscience, 18*(18), 7426–7435. http://dx.doi.org/10.1073/pnas.95.3.831.

Cox, D. D., Meier, P., Oertelt, N., & DiCarlo, J. J. (2005). "Breaking" position-invariant object recognition. *Nature Neuroscience, 8*(9), 1145–1147. http://dx.doi.org/10.1038/nn1519.

Das, A., Tadin, D., & Huxlin, K. R. (2014). Beyond blindsight: properties of visual re-learning in cortically blind fields. *The Journal of Neuroscience, 34*(35), 11652–11664. http://dx.doi.org/10.1523/JNEUROSCI.1076-14.2014.

Denison, R. N., Heeger, D. J., & Carrasco, M. (2017). Attention flexibly trades off across points in time. *Psychonomic Bulletin & Review, 24*(4), 1142–1151. http://dx.doi.org/10.3758/s13423-016-1216-1.

Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research Psychologische Forschung, 72*(6), 630–640. http://dx.doi.org/10.1007/s00426-008-0165-3.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research, 36*(12), 1827–1837.

Deveau, J., & Seitz, A. R. (2014). Applying perceptual learning to achieve practical changes in vision. *Frontiers in Psychology, 5*(226), 2087. http://dx.doi.org/10.3389/fpsyg.2014.01166.

Donovan, I., Szpiro, S., & Carrasco, M. (2015). Exogenous attention facilitates location transfer of perceptual learning. *Journal of Vision, 15*(10), 1–16. http://dx.doi.org/10.1167/15.10.11.

Dorr, M., & Bex, P. J. (2013). Peri-saccadic natural vision. *Journal of Neuroscience, 33*(3), 1211–1217. http://dx.doi.org/10.1523/JNEUROSCI.4344-12.2013.

Dosher, B. A., Han, S., & Lu, Z.-L. (2010). Perceptual learning and attention: Reduction of object attention limitations with practice. *Vision Research, 50*(4), 402–415. http://dx.doi.org/10.1016/j.visres.2009.09.010.

Dunkley, B. T., Baltaretu, B., & Crawford, J. D. (2016). Trans-saccadic interactions in human parietal and occipital cortex during the retention and comparison of object orientation. *Cortex, 82*, 263–276. http://dx.doi.org/10.1016/j.cortex.2016.06.012.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences USA, 103*(18), 7192–7197. http://dx.doi.org/10.1073/pnas.0509557103.

Fahle, M., & Edelman, S. (1993). Long-term learning in vernier acuity: Effects of stimulus orientation, range and of feedback. *Vision Research, 33*(3), 397–412. http://dx.doi.org/10.1016/0042-6989(93)90094-D.

Fairhall, S. L., Schwarzbach, J., Lingnau, A., Van Koningsbruggen, M. G., & Melcher, D. (2017). Spatiotopic updating across saccades revealed by spatially-specific fMRI adaptation. *Neuroimage, 147*, 339–345. http://dx.doi.org/10.1016/j.neuroimage.2016.11.071.

Findlay, J. M., & Gilchrist, I. D. (2003). *Active vision.* Oxford University Press.

Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature, 287*(5777), 43–44. http://dx.doi.org/10.1038/287043a0.

Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research, 21*(7), 1149–1158.

Ganmor, E., Landy, M. S., & Simoncelli, E. P. (2015). Near-optimal integration of orientation information across saccades. *Journal of Vision, 15*(16), 1–12. http://dx.doi.org/10.1167/15.16.8.

Harrison, W. J., Retell, J. D., Remington, R. W., & Mattingley, J. B. (2013). Visual crowding at a distance during predictive remapping. *Current Biology, 23*(9), 793–798. http://dx.doi.org/10.1016/j.cub.2013.03.050.

He, D., Mo, C., & Fang, F. (2017). Predictive feature remapping before saccadic eye movements. *Journal of Vision, 17*(5), 1–12. http://dx.doi.org/10.1167/17.5.14.

Herrmann, K., Montaser-Kouhsari, L., Carrasco, M., & Heeger, D. J. (2010). When size matters: Attention affects performance by contrast or response gain. *Nature Neuroscience, 13*(12), 1554–1559. http://dx.doi.org/10.1038/nn.2669.

Herwig, A., & Schneider, W. X. (2014). Predicting object features across saccades:

Evidence from object recognition and visual search. *Journal of Experimental Psychology: General, 143*(5), 1903–1922. http://dx.doi.org/10.1037/a0036781.

Herwig, A., Weiss, K., & Schneider, W. X. (2015). When circles become triangular: How transsaccadic predictions shape the perception of shape. *Annals of the New York Academy of Sciences, 1339*(1), 97–105. http://dx.doi.org/10.1111/nyas.12672.

Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception and Psychophysics, 57*(6), 787–795.

Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception and Psychophysics, 45*(2), 162–174. http://dx.doi.org/10.3758/BF03208051.

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. http://dx.doi.org/10.1523/JNEUROSCI.0745-14.2014.

Hunt, A. R., & Cavanagh, P. (2011). Remapped visual masking. *Journal of Vision, 11*(1), 1–8. http://dx.doi.org/10.1167/11.1.13.

Jeter, P. E., Dosher, B. A., Petrov, A., & Lu, Z. L. (2009). Task precision at transfer determines specificity of perceptual learning. *Journal of Vision, 9*(3), 1–13. http://dx.doi.org/10.1167/9.3.1.

Jonikaitis, D., & Theeuwes, J. (2013). Dissociating oculomotor contributions to spatial and feature-based selection. *Journal of Neurophysiology, 110*, 1525–1534.

Jonikaitis, D., Szinte, M., Rolfs, M., & Cavanagh, P. (2013). Allocation of attention across saccades. *Journal of Neurophysiology, 109*(5), 1425–1434.

Kalogeropoulou, Z., & Rolfs, M. (2017). Saccadic eye movements do not disrupt the deployment of feature-based attention. *Journal of Vision, 17*(8), 1–15. http://dx.doi.org/10.1167/17.8.4.

Kingdom, F. A. A., & Prins, N. (2016). *Psychophysics: A practical introduction* (2nd ed.). London: Academic Press.

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3. *Perception, 36*, 14.

Knapen, T., Swisher, J. D., Tong, F., & Cavanagh, P. (2016). Oculomotor remapping of visual information to foveal retinotopic cortex. *Frontiers in Systems Neuroscience, 10*, 13992. http://dx.doi.org/10.3389/fnsys.2016.00054.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*(13), 1897–1916.

Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature, 403*(6772), 892–895. http://dx.doi.org/10.1038/35002588.

Lescroart, M. D., Kanwisher, N., & Golomb, J. D. (2016). No evidence for automatic remapping of stimulus features or location found with fMRI. *Frontiers in Systems Neuroscience, 10*, 150. http://dx.doi.org/10.3389/fnsys.2016.00053.

Levi, D. M., & Li, R. W. (2009). Perceptual learning as a potential treatment for amblyopia: A mini-review. *Vision Research, 49*(21), 2535–2549. http://dx.doi.org/10.1016/j.visres.2009.02.010.

Levi, D. M., & Polat, U. (1996). Neural plasticity in adults with amblyopia. *Proceedings of the National Academy of Sciences USA, 93*(13), 6830–6834.

Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *The Journal of the Acoustical Society of America, 49*(2), 467.

Li, H.-H., Barbot, A., & Carrasco, M. (2016). Saccade preparation reshapes sensory tuning. *Current Biology, 26*(12), 1564–1570. http://dx.doi.org/10.1016/j.cub.2016.04.028.

Li, W. (2016). Perceptual learning: Use-dependent cortical plasticity. *Annual Review of Vision Science, 2*(1), 109–130. http://dx.doi.org/10.1146/annurev-vision-111815-114351.

Ling, S., Liu, T., & Carrasco, M. (2009). How spatial and feature-based attention affect the gain and tuning of population responses. *Vision Research, 49*(10), 1194–1204. http://dx.doi.org/10.1016/j.visres.2008.05.025.

Lu, Z. L., Lin, Z., & Dosher, B. A. (2016). Translating perceptual learning from the laboratory to applications. *Trends in Cognitive Sciences, 20*(8), 561–563. http://dx.doi.org/10.1016/j.tics.2016.05.007.

Lu, Z.-L., Hua, T., Huang, C.-B., Zhou, Y., & Dosher, B. A. (2011). Visual perceptual learning. *Neurobiology of Learning and Memory, 95*(2), 145–151. http://dx.doi.org/10.1016/j.nlm.2010.09.010.

Marino, A. C., & Mazer, J. A. (2016). Perisaccadic updating of visual representations and attentional states: Linking behavior and neurophysiology. *Frontiers in Systems Neuroscience, 10*(10), 11. http://dx.doi.org/10.3389/fnsys.2016.00003.

Matin, L., & Pearce, D. G. (1965). Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. *Science, 148*(3676), 1485–1488. http://dx.doi.org/10.1126/science.148.3676.1485.

Medendorp, W. P., Goltz, H. C., & Vilis, T. (2005). Remapping the remembered target location for anti-saccades in human posterior parietal cortex. *Journal of Neurophysiology, 94*(1), 734–740. http://dx.doi.org/10.1152/jn.01331.2004.

Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *Journal of Neuroscience, 23*(15), 6209–6214.

Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience, 10*(7), 903–907. http://dx.doi.org/10.1038/nn1917.

Melcher, D., & Colby, C. L. (2008). Trans-saccadic perception. *Trends in Cognitive Sciences, 12*(12), 466–473. http://dx.doi.org/10.1016/j.tics.2008.09.003.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2003). Spatial updating in human parietal cortex. *Neuron, 39*(2), 361–373.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2007). Remapping in human visual cortex. *Journal of Neurophysiology, 97*(2), 1738–1755. http://dx.doi.org/10.1152/jn.00189.2006.

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision, 7*(14), 1–16. http://dx.doi.org/10.1167/7.14.8.

Ohl, S., Kuper, C., & Rolfs, M. (2017). Selective enhancement of orientation tuning before saccades. *Journal of Vision, 17*(13), 1–11. http://dx.doi.org/10.1167/17.13.2.

Paeye, C., Collins, T., & Cavanagh, P. (2017). Transsaccadic perceptual fusion. *Journal of Vision, 17*(1), 14–18. http://dx.doi.org/10.1167/17.1.14.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Pelli, D. G., & Cavanagh, P. (2013). Object recognition: Visual crowding from a distance. *Current Biology, 23*(11), R478–9. http://dx.doi.org/10.1016/j.cub.2013.04.022.

Petrov, A. A., & Hayes, T. R. (2010). Asymmetric transfer of perceptual learning of luminance- and contrast-modulated motion. *Journal of Vision, 10*(14), 1–22. http://dx.doi.org/10.1167/10.14.11.

Polat, U., Ma-Naim, T., Belkin, M., & Sagi, D. (2004). Improving vision in adult amblyopia by perceptual learning. *Proceedings of the National Academy of Sciences USA, 101*(17), 6692–6697. http://dx.doi.org/10.1073/pnas.0401200101.

Prins, N., & Kingdom, F. A. A. (n.d.). Palamedes: Matlab routines for analyzing psychophysical data. Retrieved from http://www.palamedestoolbox.org.

Puntiroli, M., Kerzel, D., & Born, S. (2015). Perceptual enhancement prior to intended and involuntary saccades. *Journal of Vision, 15*(4), 1–14. http://dx.doi.org/10.1167/15.4.2.

Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience, 32*(40), 13744–13752.

Rolfs, M., & Szinte, M. (2016). Remapping attention pointers: Linking physiology and behavior. *Trends in Cognitive Sciences, 20*(6), 399–401. http://dx.doi.org/10.1016/j.tics.2016.04.003.

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience, 14*(2), 252–256. http://doi.org/http://dx.doi.org/10.1038/nn.2711.

Rolfs, M., Murray-Smith, N., & Carrasco, M. (2012). Perceptual learning at the location of predictive remapping. *Perception, 41*(1 Suppl), 55.

Rolfs, M., Murray-Smith, N., & Carrasco, M. (2013). Perceptual learning through remapping: How presaccadic updating affects visual processing. *Perception, 42*(1 Suppl), 160.

Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature, 386*(6625), 598–601. http://dx.doi.org/10.1038/386598a0.

Sagi, D. (2011). Perceptual learning in vision research. *Vision Research, 51*(13), 1552–1566. http://dx.doi.org/10.1016/j.visres.2010.10.019.

Sasaki, Y., Nanez, J. E., & Watanabe, T. (2009). Advances in visual perceptual learning and plasticity. *Nature Reviews Neuroscience, 11*(1), 53–60. http://dx.doi.org/10.1038/nrn2737.

Szinte, M., Carrasco, M., Cavanagh, P., & Rolfs, M. (2015). Attentional trade-offs maintain the tracking of moving objects across saccades. *Journal of Neurophysiology, 113*(7), 2220–2231. http://dx.doi.org/10.1152/jn.00966.2014.

Szinte, M., Jonikaitis, D., Rolfs, M., Cavanagh, P., & Deubel, H. (2016). Presaccadic motion integration between current and future retinotopic locations of attended objects. *Journal of Neurophysiology, 116*(4), 1592–1602. http://dx.doi.org/10.1152/jn.00171.2016.

Szpiro, S. F. A., & Carrasco, M. (2015). Exogenous attention enables perceptual learning. *Psychological Science, 26*(12), 1854–1862. http://dx.doi.org/10.1177/0956797615598976.

Szpiro, S., Spering, M., & Carrasco, M. (2014). Perceptual learning modifies untrained pursuit eye movements. *Journal of Vision, 14*(8), 1–13. http://dx.doi.org/10.1167/14.8.8.

Talgar, C. P., Pelli, D. G., & Carrasco, M. (2004). Covert attention enhances letter identification without affecting channel tuning. *Journal of Vision, 4*(1), 22–31. http://dx.doi.org/10.1167/4.1.3.

Thakkar, K. N., Diwadkar, V. A., & Rolfs, M. (2017). Oculomotor prediction: A window into the psychotic mind. *Trends in Cognitive Sciences, 21*(5), 344–356. http://dx.doi.org/10.1016/j.tics.2017.02.001.

Valsecchi, M., & Gegenfurtner, K. R. (2016). Dynamic re-calibration of perceived size in fovea and periphery through predictable size changes. *Current Biology, 26*(1), 59–63. http://dx.doi.org/10.1016/j.cub.2015.10.067.

Volkmann, F. C., Riggs, L. A., White, K. D., & Moore, R. K. (1978). Contrast sensitivity during saccadic eye movements. *Vision Research, 18*(9), 1193–1199.

Wang, R., Zhang, J.-Y., Klein, S. A., Levi, D. M., & Yu, C. (2012). Task relevancy and demand modulate double-training enabled transfer of perceptual learning. *Vision Research, 61*, 33–38. http://dx.doi.org/10.1016/j.visres.2011.07.019.

Wang, R., Zhang, J.-Y., Klein, S. A., Levi, D. M., & Yu, C. (2014). Vernier perceptual learning transfers to completely untrained retinal locations after double training: A "piggybacking" effect. *Journal of Vision, 14*(13), 1–10. http://dx.doi.org/10.1167/14.13.12.

White, A. L., Rolfs, M., & Carrasco, M. (2013). Adaptive deployment of spatial and feature-based attention before saccades. *Vision Research, 85*, 26–35. http://dx.doi.org/10.1016/j.visres.2012.10.017.

Wijdenes, L. O., Marshall, L., & Bays, P. M. (2015). Evidence for optimal integration of visual feature representations across saccades. *Journal of Neuroscience, 35*(28), 10146–10153. http://dx.doi.org/10.1523/JNEUROSCI.1040-15.2015.

Wolf, C., & Schütz, A. C. (2015). Trans-saccadic integration of peripheral and foveal feature information is close to optimal. *Journal of Vision, 15*(16), 1–118. http://dx.doi.org/10.1167/15.16.1.

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*(24), 1922–1926.

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision, 4*, 169–182. http://dx.doi.org/10.1167/4.3.4.

Zhang, E., & Li, W. (2010). Perceptual learning beyond retinotopic reference frame. *Proceedings of the National Academy of Sciences USA, 107*(36), 15969–15974.

Zhang, E., Zhang, G.-L., & Li, W. (2013). Spatiotopic perceptual learning mediated by retinotopic processing and attentional remapping. *European Journal of Neuroscience, 38*, 3758–3767.

Zhang, G.-L., Cong, L.-J., Song, Y., & Yu, C. (2013). ERP P1–N1 changes associated with Vernier perceptual learning and its location specificity and transfer. *Journal of Vision, 13*(4), 1–13. http://dx.doi.org/10.1167/13.4.19.

Zhang, T., Xiao, L.-Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Decoupling location specificity from perceptual learning of orientation discrimination. *Vision Research, 50*(4), 368–374. http://dx.doi.org/10.1016/j.visres.2009.08.024.