Perceptual learning across saccades: Feature but not location specific

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Perceptual learning is the ability to enhance perception through practice. The hallmark of perceptual learning is its specificity for the trained location and stimulus features, such as orientation. For example, training in discriminating a grating's orientation improves performance only at the trained location but not in other untrained locations. Perceptual learning has mostly been studied using stimuli presented briefly while observers maintained gaze at one location. However, in everyday life, stimuli are actively explored through eye movements, which results in successive projections of the same stimulus at different retinal locations. Here, we studied perceptual learning of orientation discrimination across saccades. Observers were trained to saccade to a peripheral grating and to discriminate its orientation change that occurred during the saccade. The results showed that training led to transsaccadic perceptual learning (TPL) and performance improvements which did not generalize to an untrained orientation. Remarkably, however, for the trained orientation, we found a complete transfer of TPL to the untrained location in the opposite hemifield suggesting high flexibility of reference frame encoding in TPL. Three control experiments in which participants were trained without saccades did not show such transfer, confirming that the location transfer was contingent upon eye movements. Moreover, performance at the trained location, but not at the untrained location, was also improved in an untrained fixation task. Our results suggest that TPL has both, a location-specific component that occurs before the eye movement and a saccade-related component that involves location generalization.

perceptual learning | eye movements | transsaccadic perception | perception action | generalization

Significance

For decades, visual perceptual learning was mainly studied without considering its connection to eye movements and was characterized by its specificity to the trained location and stimulus features. In contrast, our study presents a different view of perceptual learning within an active, ecological framework (i.e., across eye movements), which generalizes to an untrained location in the opposite visual hemifield. Our findings suggest that this type of transsaccadic perceptual learning has both retinotopic and nonretinotopic components and allows a more flexible generalization than found in the classic, fixation-based paradigms. Our results challenge current models of perceptual learning that do not incorporate saccade-related mechanisms, as well as models of transsaccadic perception that do not account for perceptual learning.

Perceptual learning refers to the ability to improve perception through practice. Historically, the hallmark of perceptual learning has been its specificity for the trained stimulus feature and location. For example, improvement through training with stimuli at a given orientation does not improve performance with the same but orthogonally orientated stimuli (1–8). Moreover, perceptual learning has been found to be specific to the trained location and does not transfer to untrained retinal locations (9–12). With few exceptions (13–17), the effects of eye movements were intentionally excluded by short stimulus presentations or by a secondary irrelevant task at fixation. In these paradigms, only one stimulus was presented at one location that participants need to detect, discriminate, or categorize. However, natural vision consists in actively exploring the surrounding environment, and saccadic eye movements play a major role in this process (18). When a saccade is performed to a stimulus, it is continuously projected at different retinal locations (19). Initially, the stimulus is projected onto the peripheral or parafoveal retina (presaccadic stimulus) and then, after being dragged across the retina throughout the saccade (20), the same stimulus is projected onto the fovea (postsaccadic stimulus). Interestingly, there is a growing body of evidence that suggests the existence of mechanisms that preserve the presaccadic stimulus signals across saccades and integrate them with postsaccadic signals (21–28).

While the postsaccadic information is physically present upon saccade landing, the information of the presaccadic stimulus must rely on signals maintained across the saccade. This has been suggested to occur through predictive coding (24, 26, 28–32). Predictive coding models assume a feedforward propagation of the signal from low to high brain areas and a predictive feedback signal from high to low brain areas (33). Recent evidence suggests that these predictive signals of presaccadic features might even be available before saccade execution (34). Moreover, across an eye movement, these predictive presaccadic signals must undergo a transformation of their spatial reference frame to match the postsaccadic foveal projection of the same object. Although neural mechanisms underlying this transformation are not yet understood, a growing body of evidence supports such transformation that allows a spatiotopic encoding of pre- and postsaccadic signals. For example, human neuroimaging studies have shown repetition suppression of visual features (orientation) occurring at spatiotopic locations (31, 35). Using single-cell recordings in

rhesus macaques, Subramanian and Colby (36) found that neurons in the lateral intraparietal cortex can remap stimulus shape selectivity. Finally, Sasaki et al. (37) demonstrated that neurons in the ventral intraparietal area can flexibly adapt to task demands and encode object motion information in both head- and world-centered coordinates, providing evidence that the reference frame of neural representations can be flexible.

We here hypothesized that given that the encoding of the presaccadic signal transforms from a retinal to an allocentric reference frame, any transsaccadic perceptual learning (TPL) that uses these mechanisms would not be retinotopic and therefore yield more transfer across locations. To test this, we investigated whether training to discriminate orientation changes across saccades leads to perceptual learning in the first place, as it does in fixation paradigms. Second, we tested whether the potential TPL is orientation and location specific. Third, we analyzed whether the learning generalizes to fixation conditions. Our results indeed showed perceptual learning for transsaccadic orientation change discrimination. This transsaccadic learning was orientation specific but transferred completely to the untrained hemifield in the saccade condition.

Methods

General Methods.

Participants. Forty-five naive participants (mean age 25, age range 18 to 32; 27 males) were recruited, nine for each of the five experiments. Prior to the experiments, participants signed informed consent and were compensated 10€/hour for their participation. All procedures were in accordance with the Declaration of Helsinki and were approved by the local ethical committee (LMU München and HU Berlin).

Setup. Participants sat in a quiet and dimly illuminated room, resting their head on a chinrest. The experiments were controlled by a PC, connected with an EyeLink 1000 (SR Research Ltd.) that recorded gaze position of the dominant eye with a sampling rate of 1,000 Hz. Stimuli were displayed at a 1,920 × 1,080 pixel resolution and a 240-Hz refresh rate on a BenQ Zowie XL2540, LCD monitor (51.5 × 29 cm), linearized with a Minolta CS-100 luminance meter (Osaka, Japan) in Exps. 1 to 4 and a ViewPixx 3D, LCD monitor (VPixx Technologies, Quebec, Canada; 52.5 × 29.5 cm) with a 120-Hz refresh rate in Exp. 5. The display, eye tracking, and response collection from a standard keyboard were controlled using Matlab (The MathWorks, Natick, MA) with Psychophysics (38, 39), EyeLink (40) and Palamedes (41) toolboxes. The viewing distance was 100 cm except in Exp. 5 where it was 57 cm.

Stimuli. The fixation was a 0.8 dva (degrees of visual angle) diameter "bull's eye" composed of superimposed black (~0 cd/m^2) and white (60 cd/m^2) disks (Fig. 1B). Targets were square-wave gratings with a spatial frequency of 3 cycles/1 dva. The stripes of the grating were black (~0 cd/m^2) and white (60 cd/m^2) and the grating radius was 3 dva with a circular Gaussian envelope. Stimuli were presented on a uniform, gray background (30 cd/m^2).

Procedure. All experiments were conducted on five consecutive days, if possible (Fig. 1C). On the first day, the participants familiarized themselves with the setup and task by performing a block of 80 warm-up trials. Afterward, the baseline performance for various fixation and saccade conditions was determined through pretraining tests, each consisting of a single block of 80 trials, and randomized across participants. After a break of at least 1 h, participants underwent the first training session of 12 blocks of 80 trials. They continued to train with one training session per day (12 blocks of 80 trials each) over the next 3 d. On the final, fifth day, participants took the posttraining tests, which were identical to the pretraining tests and presented in a random order.

Each trial began with the fixation bull's eye presented in the center of the screen that participants had to fixate for at least 200 ms within a virtual circle of 2 dva of radius (e.g., Fig. 1 A and D). Participants continued to fixate on the bull's eye for a duration chosen randomly between 400 and 700 ms. Then, the first grating was presented at a distance of 8 dva (screen center to grating center) either on the right (L1) or left (L2) side of the fixation. The orientation of the first grating was chosen randomly from trial to trial from a uniform distribution comprising angles of 40° to 50° degrees (O1) or −40° to −50° (O2) with respect to the upper-vertical or north (0°) in steps of 1°. The combination of location and orientation varied among the different conditions, as described below and shown in Fig. 1 A and B

(Exp. 1) and Fig. 2C (Exp. 2). The trial procedure then differed between saccade and fixation conditions (shown in red and blue, respectively in the figures).

In the saccade conditions, participants executed a saccade to the grating's center. Once the saccade onset was detected, defined as the first gaze sample moving outside a virtual circle with a 2 dva of radius around the fixation, the first grating was swapped with the second grating. The second grating differed from the first grating in orientation in a clockwise or counterclockwise direction (chosen at random) and was presented for 300 ms. The orientation change between the two gratings was chosen from a uniform prior distribution (ranging from 0.1° to 20° with a step of 0.1°) and controlled by an adaptive staircase procedure, ensuring 75% of correct responses [best PEST; (42)]. Participants reported the orientation change of the grating (clockwise or counterclockwise) by pressing either the left or right arrow button on the keyboard, respectively. Incorrect answers were followed by auditory feedback. After a 500-ms delay, the next trial started. The adaptive staircase procedure excluded trials in which participants made saccades before the first grating onset outside of the 2-dva radius fixation area or earlier than 50 ms or later than 350 ms after the first grating onset. Additionally, trials were excluded if participants blinked during the trial, as well as trials in which saccades that did not land inside a 2-dva radius area centered on the second grating or did not stay within that area for at least 50 ms after crossing its boundary. All these excluded trials were repeated at the end of the same block.

In the fixation conditions, participants kept fixation within the 2-dva radius area around the screen center throughout the whole trial. The first grating was presented for 300 ms, then removed from the screen while only a fixation was presented for 200 ms, followed by the presentation of the second grating for 300 ms. As in the saccade condition, the second grating differed in orientation from the first grating. This short, 200 ms break was included to increase task difficulty as previously shown (43). The rest of the procedure was identical to the saccade condition. Trials in which participants executed a saccade outside of the 2 dva radius area around fixation or blinked during the trial were excluded from the staircase procedure and were repeated at the end of the same block.

Each block contained 80 trials which were correct according to the eye-movement or fixation criteria described above. Participants could take breaks between the blocks.

Warm-up. The warm-up consisted of one block of 80 trials during which participants saccaded to the first grating presented at location 2 with orientation 2 to discriminate the orientation change occurring during the saccade. Importantly, this location-orientation combination (L2O2) was different from the subsequent training and the pre- and post-training tests to avoid interference with them.

Training. During training, participants were presented with stimuli only at location 1 with the orientation range 1 (+40° to +50°) to which they had to make an eye movement (hence condition sacL1O1) and judge the orientation change occurring during the eye movement. Each training session comprised 12 training blocks. The learning was assessed by transforming the mean threshold.

Experiment 1. Before training, participants' baseline performance was measured in four pretraining test conditions. Each condition was tested in a separate block (Fig. 1B). In the untrained orientation condition (sacL1O2), participants performed saccades to gratings at location 1 (L1), the same location as during training, but with untrained gratings orientations (O2), orthogonal to the trained ones. In the untrained location condition (sacL2O1), participants saccaded to gratings with the trained orientation, but these were presented at the untrained location 2. Baseline performance was also tested in a fixation condition with two peripheral gratings presented at the trained location and with the trained orientation (fixL1O1). Hence, the presentation was the same as during the training, but participants kept fixating the central fixation throughout the trial. Finally, the participants were tested in a saccade-mimicking fixation condition (fixSML1O1), where the first grating was presented at the trained location (L1) while the second grating was presented at the fixation location, thus mimicking the sequence of retinal input of the trained saccade condition. That is, similarly to the trained saccade condition, the retina was first stimulated in the periphery and then, after the saccade, in the foveal and parafoveal region.

Experiment 2. The second experiment followed the same procedure as Exp. 1, including three pre- and post-training test conditions: the sacL1O1, sacL2O1, and fixL1O1. Additionally, in order to test how flexible the generalization of TPL to
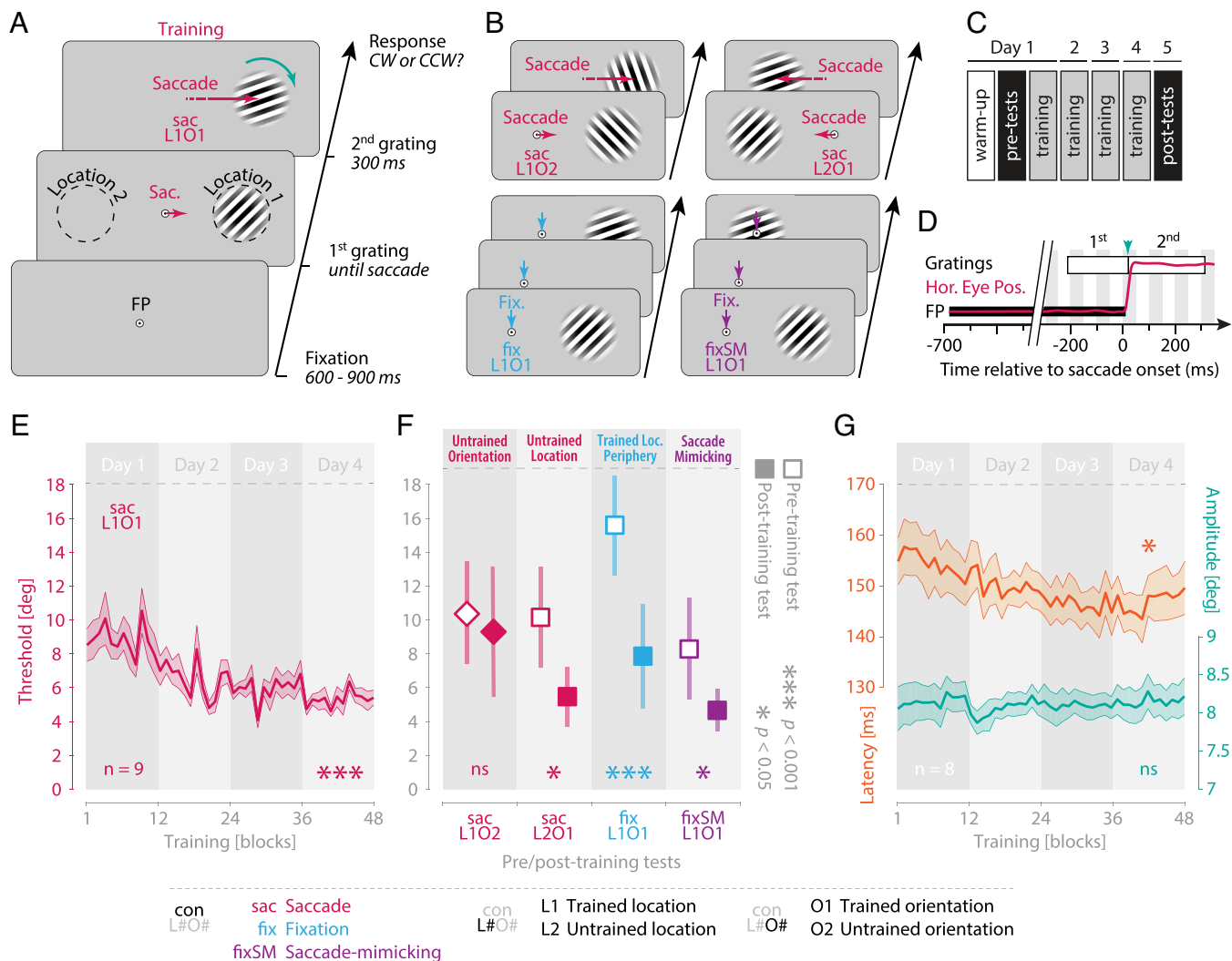
Fig. 1. Experiment 1. (*A*) Training trial procedure. After fixating the fixation point (FP), the first grating with a random orientation within the range of 45 ± 10° (orientation 1 or O1) was shown at the location 1 (L1). Participants saccaded to its center which triggered the presentation of the second grating differing in orientation either in the clockwise (like in the example, symbolized by the green arrow) or counterclockwise direction. Participants reported the direction of the orientation change after the eye movement. (*B*) In the pre- and post-training tests, participants performed the orientation change discrimination task as during training, however with different location–orientation combinations. In the two saccade (sac) conditions, participants were tested with the untrained, orthogonal orientations at the trained location (sacL1O2) and the trained orientations at the untrained location (sacL2O1). In the two fixation (fix) conditions, participants kept fixation in the screen center throughout the trial. In the fixL1O1 condition, both the first and the second gratings were presented at the trained location (L1). In the fixSML1O1 condition, the first grating was presented at the trained location (L1) while the second grating was presented at the fixation location, mimicking the retinal input of a saccade, such as during a typical training trial (sacL1O1). (*C*) Experiments were conducted on five days. On day 1, participants were first familiarized with the setup and task within one warm-up block. Then, the baseline performance was measured in the pretraining tests followed by the first training session. Training continued on days 2, 3, and 4, one session a day, each consisting of 12 blocks of 80 trials. On the fifth day, participants underwent the post-training tests. (*D*) Time course for a typical saccade trial. The red line symbolizes horizontal eye position relative to saccade onset (Hor. Eye Pos.). White rectangles illustrate the timing of the first and the second gratings with the green arrow marking the orientation change. Black rectangle symbolizes the fixation point timing (FP). (*E*) Training led to TPL; Block mean thresholds ± 1 SEM. (*F*) Transsaccadic orientation discrimination thresholds across different pre- and post-training tests. TPL did not transfer to untrained orientations (sacL1O2). Remarkably however, TPL fully transferred to the untrained location (sacL2O1). Additionally, there was a strong transfer to the untrained fixation condition (fixL1O1) as well as in the saccade-mimicking condition (fixSML1O1). Mean thresholds ± 95% CI. (*G*) Saccade latencies significantly decreased through training but were not correlated with performance. Block means ± 1 SEM.

untrained locations is, two new conditions were included (Fig. 2*C*). In the saccade condition (sacL1+2), participants were presented with trained orientation gratings (O1), with the first grating presented at the trained location (L1). However, participants were asked to saccade to a small black dot presented at location 2. As soon as the saccade was detected, that black dot was replaced by the second grating. This condition allowed us to disentangle the orientation signal from the saccade target and to test whether the location transfer needs to occur in the same spatiotopic location. In the last transfer condition (fixL2O1), participants were presented with two peripheral gratings with the trained orientations (O1) but at the untrained location (L2) while participants maintained fixation throughout the trial.

The three control experiments (Exps. 3 to 5) followed the same general procedure as Exps. 1 and 2. More detailed information can be found in *SI Appendix*.

Results

Experiment 1. Results from Exp. 1 are shown in the lower panels of Fig. 1. Perceptual learning typically develops rapidly at the beginning and then decelerates over time. To capture this, we employ log-log transformed linear regression to individual, 48 training thresholds. One sample *t* tests tested the null hypothesis whether the slopes of these regression lines were not different from zero. All participants showed significant negative regression slopes, demonstrating perceptual learning (Fig. 1*E*; slope = –0.19 ± 0.09 (mean ± SD), $t_{[8]}$ = 6.65, P = 0.0002, d = 3.13). Perceptual learning did not transfer to the untrained, orthogonal orientations
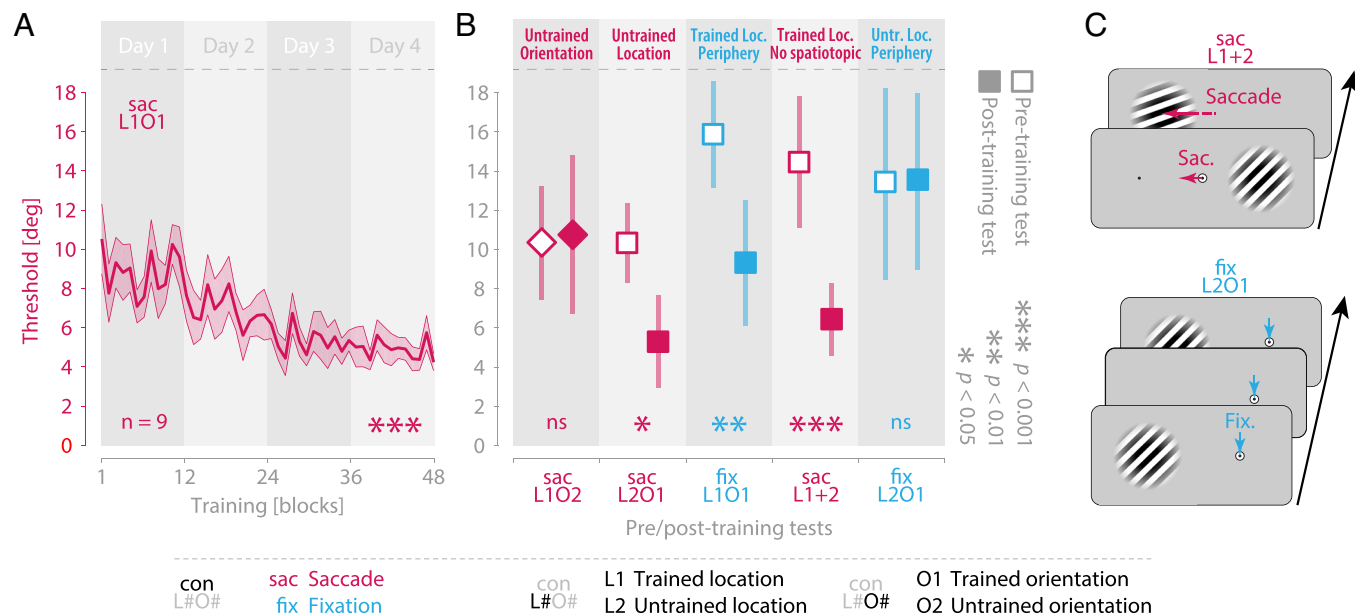
Fig. 2. Experiment 2. (*A*) Performance at discriminating transsaccadic orientation changes improved through training, demonstrating TPL. Block means ± 1 SEM. (*B*) TPL was orientation specific (sacL1O2) but, as in Experiment 1, it fully transferred to the untrained location (sacL2O1). Additionally, there was also a strong transfer to the untrained fixation condition (fixL1O1) but not when probed at the untrained location 2 (fixL2O1). Finally, learning transferred to the nonspatiotopic saccade condition (sacL1+2) demonstrating the flexible characteristics of TPL. Mean thresholds ± 95% CI. (*C*) In the sacL1+2 condition, the first grating was presented at the trained location (L1) while the participants made a saccade to a small dot at location 2 (L2). The saccade onset triggered the presentation of the second grating at location 2 (L2). In the fixL2O1 condition, both gratings were presented with the trained orientation (O1) but at the untrained location (L2).

presented at the trained location (Fig. 1*F*, sacL1O2; pre = 10.36 ± 1.60 vs. post = 9.31 ± 2.08, $F_{[1,8]}$ = 0.97, P = 0.354, d = 0.19). Remarkably, however, training strongly improved performance at the untrained location when tested with the trained orientation (Fig. 1*F*, sacL2O1; pre = 10.16 ± 1.61 vs. post = 5.47 ± 0.95, $F_{[1,8]}$ = 19.08, P = 0.002, d = 1.18). Moreover, training improved performance in the fixation condition when both gratings were presented at the trained location (Fig. 1*F*; fixL1O1; pre = 15.60 ± 1.58 vs. post = 7.83 ± 1.66, $F_{[1,8]}$ = 52.47, P = 0.00009, d = 1.60). Finally, in the saccade mimicking condition, the improvement was significant (Fig. 1*F*; fixSML1O1, pre = 8.29 ± 1.62 vs. post = 4.66 ± 0.68, $F_{[1,8]}$ = 11.41, P = 0.017, d = 0.97). Unlike saccade amplitudes that remained unchanged, saccade latencies significantly decreased throughout the training (Fig. 1*G*, slope = −0.21 ± 0.07, $t_{[7]}$ = 3.18, P = 0.016, d = 1.12).

Experiment 2. Experiment 2 aimed at replicating the main results of Experiment 1 while testing additional conditions that would provide insight into the nature and extent of saccade-related transfer. Participants improved performance through training (Fig. 2*A*; slope = −0.19 ± 0.08, $t_{[8]}$ = 7.25, P = 0.0001, d = 3.42). This TPL did not transfer to the untrained orientation (sacL1O2; pre = 10.34 ± 1.55 vs. post = 10.76 ± 2.17, $F_{[1,8]}$ = 0.05, P = 0.822, d = 0.07; Fig. 2*B*). Importantly however, with saccades, TPL transferred to the untrained location with the trained orientation (sacL2O1), thus replicating the main finding from the previous experiment (sacL2O1; pre = 10.36 ± 1.08 vs. post = 5.30 ± 1.27, $F_{[1,8]}$ = 8.08, P = 0.022, d = 1.43). TPL also transferred to the fixation condition at the trained location (fixL1O1; pre = 15.88 ± 1.46 vs. post = 9.33 ± 1.72, $F_{[1,8]}$ = 4.90, P = 0.006, d = 1.37) as well as to the nonspatiotopic saccade condition (Fig. 2*C*), in which pre- and post-saccadic stimuli were shown in different spatial locations (sacL1+2; pre = 14.46 ± 1.81 vs. post = 6.45 ± 1.00, $F_{[1,8]}$ = 20.29, P = 0.0003, d = 1.83). Finally, with mere fixation, there was no transfer of learning to the fixL2O1 condition, in which performance was tested at the untrained location with the

trained orientation (pre = 13.34 ± 2.64 vs. post = 13.45 ± 2.42, $F_{[4,32]}$ = 0.002, P = 1.00, d = 0.02). As in Exp. 1, we found a significant decrease in saccade latencies during training (slope = −0.18 ± 0.07, $t_{[8]}$ = 2.73, P = 0.026, d = 0.91) but no change in saccade amplitude.

Control Experiments Without Eye Movements. Exps. 1 and 2 found that training on an orientation change discrimination task leads to TPL that was orientation specific but transferred to the opposite hemifield location, thus strongly contrasting with most findings of perceptual learning without eye movements. However, given that our paradigm was never used in the context of perceptual learning, our conclusions required validation against potential alternative explanations (for more details, please see *SI Appendix*).

Exp. 3 was designed to investigate whether our task yields orientation, and especially location specificity, without eye movements in the first place. Participants were trained to discriminate the orientation change between two gratings presented at the same peripheral location while fixating on the screen center (Fig. 3 *A*, *Left*; fixL1O1). Before and after training, the performance was tested for an untrained orientation (fixL1O2) and location (fixL2O1) as during training as well as in saccade and saccade-mimicking conditions for the trained orientation and location (sacL1O1 and fixSML1O1, respectively). While training significantly enhanced performance (Fig. 3*B*; slope = −0.15 ± 0.08, $t_{[8]}$ = 5.41, P = 0.0006, d = 2.55), the learning remained orientation and location specific and did not transfer to either saccade or saccade-mimicking conditions (Fig. 3*C*).

Exp. 4 tested whether improvements restricted to the foveal (and parafoveal) regions in discriminating orientations could account for TPL results. Hence, participants were trained to discriminate the orientation of a grating centered on the screen, where they fixated (Fig. 3 *A*, *Middle*). The training boosted performance (Fig. 3 *B*, *Middle*; slope = −0.21 ± 0.06, $t_{[8]}$ = 10.25,

Fig. 3. Control experiments without eye movements during training. (*A*) In Exp. 3, participants were trained to discriminate orientation changes between two gratings presented subsequently in a periphery location. In Exp. 4, Participants were trained to judge the orientation of a grating presented in the screen center as being clockwise or counterclockwise with respect to 45° In Exp. 5, the first grating was presented in the periphery (Loc. 1) while the second one was shown at fixation, mimicking the retinal input that occurs across fixations separated by a saccade. Participants were trained to discriminate the orientation change as in Exps. 1 to 4. (*B*) All three types of training led to strong ($1.51 < d < 2.03$) perceptual learning ($0.013 > P > 0.003$). Block means ± 1 SEM. (*C*) Perceptual learning (PL) in the periphery (Exp. 3, *Left*) was orientation and location specific (blue) and did not transfer to the saccade (red) or saccade-mimicking (purple) condition when the trained orientation was tested at the trained location. PL in the center of gaze (Exp. 4, *Middle*) did not transfer to any of the saccade (red) or fixation (blue and purple) conditions. Improvements in the saccade mimicking training (Exp. 5, *Right*) did not transfer to the untrained orientation and location (purple) nor the saccade condition (red). While tested with only peripheral gratings (blue), a transfer was observed for the trained orientation but not the untrained location. Block means ± 95% CI.

$P = 0.00001$, $d = 4.83$), but this improvement did not transfer to saccade (Fig. 3 *C*, *Middle*; sacL2O1, sacL1O2), saccade-mimicking (fixSML1O1) or fixation conditions (fixL1O1), suggesting that, in the absence of eye movements during training, foveal training does not result in transfer to other locations.

Finally, in Exp. 5, we tested whether TPL is saccade-contingent or can be accounted for a saccade-mimicking stimulation without eye movements. As in a saccade condition, participants were first presented with a peripheral grating, followed by a central grating,

while fixating the bull's eye (Fig. 3 *A*, *Right*). The training led to perceptual learning (Fig. 3 *B*, *Right*; slope = –0.17 ± 0.09, $t_{[8]} = 5.47$, $P = 0.0006$, $d = 2.58$). However, this perceptual learning did not generalize to untrained orientations or locations (Fig. 3 *C*, *Right*; fixSML1O2 and fixSML2O1, respectively), or the saccade condition (sacL1O1). Performance remained unchanged at the untrained location (fixL2O1) but was improved at the trained location (fixL1O1), an anticipated outcome given its inclusion in the training.

Discussion

For decades, perceptual learning was mostly studied in its simplest form, where observers were trained with brief flashes of stimuli that they needed to detect, discriminate, or categorize in binary forced choice tasks (for a review, see ref. 44). With the aim of understanding the underlying behavioral, computational, and neural processes, perceptual learning has been studied in isolation, purposely avoiding any processes involving action, including eye movements. This approach was very successful in explaining the basic findings and gave rise to eminent models (5, 45–49); it came at the cost of ecological validity, which, in contrast, is tightly linked to action (18, 50, 51).

Here, we studied perceptual learning across saccadic eye movements, what we called TPL. The training task required participants to discriminate between oriented gratings presented before and after saccades and was designed to rely on the transfer of the presaccadic information across a saccade through transsaccadic mechanisms which has been suggested to rely on predictive coding (24, 28, 30). In both main experiments (Exps. 1 and 2), training led to TPL, demonstrating that transsaccadic discrimination of orientation can be improved with practice. TPL was manifest with a saccade latency decrease, albeit that decrease was not correlated with performance ($R = 0.177$, $P = 0.496$; see *SI Appendix* for more details). Saccade amplitudes remained unchanged by the training, and there was no systematic modification of the saccade landing positions across the experiments (*SI Appendix*). Importantly, the independence of performance of saccade latency shows that TPL cannot be explained by a decrease of artifacts such as sensory adaptation. For example, it was demonstrated that presaccadic adaptation to oriented gratings builds up with time and influences the percept of the postsaccadic grating as measured by the tilt aftereffect (52).

TPL was specific to the trained orientation as previously reported in classic, fixational paradigms (1–8) and in relation to saccades (13–15). Importantly, orientation specificity demonstrates that TPL is not a result of some unspecific learning (e.g., procedural learning).

Remarkably, however, TPL transferred to the untrained location (sacL2O1) in the opposite visual hemifield of the trained location. The mean orientation discrimination thresholds from that condition (5.39 ± 0.77°; Exps. 1 and 2, combined) were in the same range as in the last training sessions (block 48; 5.11 ± 0.31°) suggesting a complete location transfer of learning. This finding strongly contrasts with previous literature that found perceptual learning to be location specific. Interestingly, TPL did not transfer to fixation conditions (fixL2O1, Exp. 2). This lack of transfer suggests that the location transfer observed in the sacL2O1 condition is linked to transsaccadic processes, possibly including predictive coding mechanisms. Furthermore, TPL was observed to transfer in the sacL1+2 condition (Exp. 2), where observers were required to saccade to a small dot in the opposite hemifield (location 2). The saccade onset triggered the displacement of the grating to the saccade landing position (location 2). TPL also transferred to that condition, which demonstrates that TPL is not limited to spatiotopic processing and that TPL encoding is highly flexible. Nevertheless, the transfer in this condition may have been influenced by the predictable location change of the grating, so it remains unclear to which extent this transfer relies on encoding flexibility or transsaccadic predictability.

Moreover, we found significant learning transfer in the fixation condition in which two successive gratings were presented at the trained location with the trained orientation (fixL1O1, Exp. 1

and 2) but not to the untrained location (fixL2O1, Exp. 2). The presence of this transfer at the trained location and its absence at the untrained location demonstrates that besides learning related to transsaccadic processing, TPL also contains a retinotopic component, similar to what has been found in classic perceptual learning paradigms. It is worth noting that this specific condition yielded the weakest performance, especially evident in Exps.1 and 2. The reason for this is not clear, with several potential explanations. First, the task required a comparison between two peripheral gratings, which is inherently more difficult than comparing a peripheral and a clear foveal grating. Second, the consistent retinal stimulation location in this condition might lead to adaptation. For example, research has shown that saccades reduce the tilt aftereffect compared to a fixation condition (53).

The most important finding in this study is the transfer of TPL to an untrained location, which was contingent on the saccade and its associated transsaccadic mechanisms. To confirm this result, we conducted a control experiment that verified that our task yielded typical orientation and location specificity without eye movements during training. Participants were trained with a task as in the fixL1O1 condition and the procedure was the same as in Exps. 1 and 2. The results confirmed location- and orientation-specific perceptual learning (Exp. 3). Additionally, a second control experiment was also conducted to ensure that TPL was not solely driven by improvements at the post-saccadic, foveal location (Exp. 4). Finally, Exp. 5 demonstrated that our results are saccade-contingent as a saccade-mimicking training without saccades did not show location generalization.

Broadly, there are two predominant theories explaining visual perceptual learning, namely the sensory retuning and the reweighting theories. Relying on the feature (e.g., orientation), location, and eye specificity, within the sensory retuning account, perceptual learning is assumed to take place at early stages of visual processing with the retuning of neurons [e.g., primary visual cortex, V1 (7, 9, 54)] where neurons are organized into orientation columns and highly retinotopic (55, 56). In the reweighting theory, perceptual learning occurs primarily beyond V1, at high levels of visual processing, by optimizing the readout (reweighting) of evidence from visual neurons along the visual hierarchy (47, 48, 57, 58). Contrarily to V1-based learning, the high-level reweighting allows less specificity as it is not bound to the rigid V1 neurons featural tuning. In the present study, we observed both, the location-specific perceptual learning occurring prior to saccades (Exp. 2; fixL2O1) and the location-unspecific, saccade-contingent perceptual learning (Exps. 1 and 2; sacL2O1). Hence, it is plausible that both, the V1-based and the high-level readout took place during TPL simultaneously. This demonstrates that these theories are not mutually exclusive as both mechanisms may be active when more ecological, sensorimotor tasks are performed.

Albeit a solid fundamental understanding of the plasticity behind perceptual learning at neural, and functional levels, translating this to practical applications (e.g., clinical) remains challenging. This is because most perceptual training protocols lead to task, stimulus, and location specificity for trained situations (44). Therefore, trainings aiming at improving patients' visual abilities can be painstaking and inefficient, given the necessity to cater to different task attributes and locations independently. For example, patients suffering from central vision loss may regain good functionality after learning to project images on their intact peripheral retina, the so-called preferred retinal locus (PRL), rather than foveating these images. In other words, patients need to learn to replace the functional role of the dysfunctional fovea with the PRL. Despite considerable improvements in the life quality of the patients, these training programs can span several years, and they

are specific to the PRL (59). A similar scenario occurs for patients with unilateral V1 damage, which induces full or partial vision loss in the contralateral visual hemifield, known as cortically induced blindness (CB). The typical recovery training for CB patients consists in a visual training at the border of the blind field adjacent to the intact visual field. Once the functionality at the trained location is recovered, the training location is progressively shifted deeper into the scotoma direction by a few degrees at most. Unfortunately, the progress acquired at one location does not transfer to the next, meaning learning begins anew (60, 61). Recently, however, it has been shown that CB patients can partially overcome the curse of the location specificity (62) using a novel double-training method that requires patients to orient attention to a location in the blind field. The double-training involves presenting two different stimulus features at two different retinal locations during the same training session (63–67). Typically, after training, perceptual learning of both features at both locations is improved but see ref (68, 69). Such perceptual learning is thought to involve high-level visual areas (63) and may occur even at a conceptual level (70). Interestingly, across a saccade, a given stimulus is projected twice at two different retinal spots, mirroring the double-training method. Moreover, a saccade triggers obligatorily the reorienting of attention toward the saccade target, which seems to be a pivotal step allowing the CB patients to improve performance at both locations (62). Hence, there is a similarity between our findings and the novel double-training paradigms, and we believe that the efficiency of double-training might come from the fact that this procedure mimics more ecologically valid conditions which naturally occur during eye movements. However, our paradigm has a unique edge over double-training: while double-training induces transfer between two trained locations (71), our paradigm elicits transfer to a location that was previously untrained. Hence, our findings could have important implications for overcoming the location specificity in clinical recovery protocols.

The transsaccadic transfer of presaccadic stimuli features (e.g., orientation) in predictive coding models is explained by a feedforward process of the presaccadic signal to higher-visual areas, which is then fed back as a predictive signal to the lower-visual areas at the predicted spatiotopic locations (29, 30). However, the precision of these predictive feedback signals is limited by the imprecise saccadic landing positions (e.g., *SI Appendix*, Fig. S4*B*). Hence, the encoding of a presaccadic memory signal should be flexible in terms of spatial location. Electrophysiological studies (37, 72) and psychophysical studies (73, 74) have shown flexible encoding of stimuli, combining both retinotopic and spatiotopic coordinates. This is also reflected in the effect of systematic manipulation of transsaccadic predictions related to saccade target size or features. This leads to perceptual recalibration of these attributes (75, 76), suggesting that the pre- and post-saccadic stimuli are merged into a single, spatially flexible representation. In line with our results that demonstrated location unspecificity of TPL, transsaccadic size recalibration was shown to transfer to the untrained location in the opposite hemifield (77, 78), further suggesting high-level visual processes and spatially flexible encoding. In accordance with that view, perceptual learning was found to occur in a nonretinotopic reference frame (14, 15, 79) and even at a conceptual level (70). Furthermore, recent studies suggest that the presaccadic predictive signal may always be mapped to the foveal and parafoveal regions, irrespectively of the saccade target location and the saccade landing site, thus reducing the complexity of the reference frame remapping across saccades (34). Indeed, Kroell and Rolfs (34) demonstrated that a peripheral saccade target feature can already be processed at fixation even before saccade

execution. This predictive signal seems to be confined to foveal and parafoveal area of roughly 5 dva. Earlier behavioral (80, 81) support that view by demonstrating foveal processing of peripheral stimuli. Indeed, a neuroimaging study (82) showed that peripheral objects are processed by the foveal retinotopic cortex. In agreement with these results, Porat and Zohary (83) found that when participants were shown briefly flashing ellipsoid stimuli occurring during saccades, they misperceived their location to be at the saccade target location. This systematic location bias persisted even after training, suggesting a robust underlying mechanism. Using the same paradigm, the authors demonstrated that training in judging the orientation of the same ellipsoid stimuli leads to perceptual learning. That perceptual learning generalized to previously untrained locations and untrained saccade directions but not to untrained tasks. This generalization has been largely attributed to the large receptive fields in V4, given that the intrasaccadic stimulus was presented in the parafoveal vicinity. In our study, we used stimuli that are known to elicit fine-tuning of V1 neurons with practice (84), and because our untrained location is in the opposite hemisphere, the broad receptive-field account cannot fully explain our observations. However, the inverse might hold true: Presaccadic predictive processes for stimuli shown before saccades might also apply to those presented when the eyes are in flight. This could explain the location generalization found by Porat and Zohary (83). Reinforcing this view, the systematic mislocalization of intrasaccadic stimuli reported by Porat and Zohary (83) has been previously identified for presaccadic stimuli (85). In this study, stimuli preceding the saccade onset by up to 250 ms were perceived to occur after the saccade when presented at the saccade target location. We propose that during TPL, presaccadic predictive signals are encoded in a flexible reference frame in higher visual areas, which allows for location transfer of stimulus orientation observed in our experiments.

Because mechanisms for transsaccadic integration have been found to be somewhat saccade specific (86), we investigated whether TPL is limited to saccade conditions. In the fixSML1O1 condition (Exp. 1), the visual input mimicked the trained saccade condition while participants kept central fixation. TPL did transfer to that condition. However, in Exp. 5, where the saccade-mimicking condition (fixSML1O1 condition) was the one that was trained, perceptual learning did not carry over to any of the saccade conditions (Fig. 3*C*). Perplexing at first sight, this discrepancy between saccade and saccade-mimicking training may be well supported by recent literature (17). Aligning with our observations, Laamerad et al. (17) showed that extensive training in motion discrimination using remapping integration mechanisms across eye movements extended this mechanism to a fixation condition—a skill absent before the training. Our findings, in tandem with the aforementioned studies, underline the distinct processes involved during passive versus active perceptual learning, demonstrating the superiority of active learning protocols regarding the transferability of acquired skills.

In summary, our study demonstrates that training orientation discrimination across eye movements leads to TPL. We propose that TPL consists of two components—a presaccadic, orientation- and location-specific component that aligns with classic visual perceptual learning and a saccade-contingent component that allows complete generalization of performance improvements to untrained locations. Our findings suggest that perceptual learning within an active-vision framework, where action and perception are intertwined, may involve distinct or additional mechanisms compared to learning in a passive-vision framework. Hence, we propose that the study of perceptual learning in a more ecological

active-vision framework may be of particular importance for the generalizability of learning protocols in sports, education, and rehabilitation (87).

Data, Materials, and Software Availability. Behavioral and eyetracking data have been deposited in the Open Science Framework (https://osf.io/hw9f5/) (88).

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