Exogenous attention facilitates perceptual learning in visual acuity to untrained stimulus locations and features

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Visual perceptual learning (VPL) refers to the improvement in performance on a visual task due to practice. A hallmark of VPL is specificity, as improvements are often confined to the trained retinal locations or stimulus features. We have previously found that exogenous (involuntary, stimulus-driven) and endogenous (voluntary, goal-driven) spatial attention can facilitate the transfer of VPL across locations in orientation discrimination tasks mediated by contrast sensitivity. Here, we investigated whether exogenous spatial attention can facilitate such transfer in acuity tasks that have been associated with higher specificity. We trained observers for 3 days (days 2–4) in a Landolt acuity task (Experiment 1) or a Vernier hyperacuity task (Experiment 2), with either exogenous precues (attention group) or neutral precues (neutral group). Importantly, during pre-tests (day 1) and post-tests (day 5), all observers were tested with neutral precues; thus, groups differed only in their attentional allocation during training. For the Landolt acuity task, we found evidence of location transfer in both the neutral and attention groups, suggesting weak location specificity of VPL. For the Vernier hyperacuity task, we found evidence of location and feature specificity in the neutral group, and learning transfer in the attention group—similar improvement at trained and untrained locations and features. Our results reveal that, when there is specificity in a perceptual acuity task, exogenous spatial attention can overcome that specificity and facilitate learning transfer to both untrained locations and features simultaneously with the same training. Thus, in addition to improving performance, exogenous attention generalizes perceptual learning across locations and features.

Introduction

As we interact with our environment, we are continuously presented with an overwhelming amount of sensory information. To make sense of this information and experience seamless perception of the visual world, we rely partly on two key mechanisms: attention and perceptual learning. Visual attention allows us to prioritize, from moment to moment, relevant information for processing while ignoring irrelevant information (for reviews, see Carrasco, 2011; Carrasco, 2014; Carrasco & Barbot, 2015; Maunsell, 2015). Visual perceptual learning (VPL) is relatively long term, allowing us to adaptively become more sensitive through increased exposure to relevant stimulus features (for review, see Sagi, 2011). Both

attention and VPL improve performance on perceptual tasks, but we are only beginning to understand how they interact.

VPL is the acquisition of visual skill, operationalized by enhanced sensitivity or discriminability, due to practice or experience with a visual task (for reviews, see Sagi, 2011; Seitz, 2017; Watanabe & Sasaki, 2015). In early infancy, highly plastic visual cortical areas functionally organize through visual experience to develop basic perceptual skills. The adult brain is less plastic, but perceptual training can still enable learning and retention of specific skills throughout the lifespan. For example, expert radiologists employ efficient search strategies when viewing medical images, such that they are faster and make fewer perceptual errors in discriminating abnormal from healthy tissue compared to novices (Waite, Grigorian, Alexander, Macknik, Carrasco, Heeger, & Martinez-Conde, 2019). Robust learning has generally been thought to require extensive and repeated training (Frank, Reavis, Tse, & Greenlee, 2014; Karni & Sagi, 1993; Watanabe, Náñez, Koyama, Mukai, Liederman, & Sasaki, 2002; Yotsumoto, Watanabe, & Sasaki, 2008), but recent studies have demonstrated long-lasting performance enhancements with short training periods (Hussain, Sekuler, & Bennett, 2011; Yashar & Carrasco, 2016; Yashar, Chen, & Carrasco, 2015).

A main property of VPL is specificity, in which performance improvements are confined to the particular trained retinal location (Ball & Sekuler, 1982; Berardi & Fiorentini, 1987; Crist, Kapadia, Westheimer, & Gilbert, 1997; Dill & Fahle, 1997; Fahle & Edelman, 1993; Fahle, Edelman, & Poggio, 1995; Jehee, Ling, Swisher, van Bergen, & Tong, 2012; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992; Yang & Maunsell, 2004; Yashar et al., 2015), stimulus feature (Adab, Popivanov, Vanduffel, & Vogels, 2014; Adini, Sagi, & Tsodyks, 2002; Ahissar & Hochstein, 1997; Batson, Beer, Seitz, & Watanabe, 2011; Berardi & Fiorentini, 1987; Fiorentini & Berardi, 1980; Fiorentini & Berardi, 1981; Jehee et al., 2012; Watanabe, Náñez, & Sasaki, 2001; Yashar & Denison, 2017), or eye (Batson et al., 2011; Karni & Sagi, 1991). For example, monocular training on a particular line orientation in one quadrant of the visual field results in local accuracy improvements on that orientation for the trained eye, and no accuracy changes in the other three quadrants, or for the untrained eye, when the relative orientation of the line is orthogonal (Karni & Sagi, 1991, but see also Schoups & Orban, 1996, who found interocular transfer). We note that in most studies there is learning specificity even when observers already know the relevant location and feature of the stimulus to be trained, and in principle observers could attend to such properties.

Learning specificity is often attributed to plasticity in sensory areas that encode precise stimulus locations and features, such as V1 (Ghose, Yang, & Maunsell, 2002; Gu et al., 2011; Schoups, Vogels, Qian, & Orban, 2001; Watanabe et al., 2002; Yotsumoto et al., 2008; Zhang, Cong, Song, & Yu, 2013), but the degree of specificity depends on training conditions and task demands (Hung & Seitz, 2014; Jeter, Dosher, Petrov, & Lu, 2009; Xiao et al., 2008; Yashar & Denison, 2017). Perceptual learning has also been related to higher cortical regions, such as the lateral intraparietal cortex (LIP) and anterior cingulate cortex (Adab & Vogels, 2011; Chowdhury & DeAngelis, 2008; Jeter, Dosher, Liu, & Lu, 2010; Kahnt, Grueschow, Speck, & Haynes, 2011; Law & Gold, 2008). Whether learning depends on changes in early cortical representations or in their connections to higher-level decision-making areas is subject to debate (Lu, Liu, & Dosher, 2010; Sotiropoulos, Seitz, & Seriès, 2011; Zhang et al., 2013). It is likely that many cortical regions and networks underlie VPL (for reviews, see Dosher & Lu, 2017; Maniglia & Seitz, 2018).

Perceptual learning of visual acuity has been reported to be highly specific. This skill is constrained by high spatial resolution, and it is considered to be mediated by low-level cortical mechanisms (Ahissar & Hochstein, 1997). Landolt-C acuity in the periphery has been shown to not improve with practice, possibly due to resolution constraints (Westheimer, 2001). Vernier offset discrimination thresholds improve with practice, but only for the trained orientation, location, or eye (Fahle, 2004; Fahle & Edelman, 1993; Fahle & Morgan, 1996; Fiorentini & Berardi, 1980; Poggio, Fahle, & Edelman, 1992; for reviews, see Sagi, 2011; Watanabe & Sasaki, 2015).

A major challenge in developing expertise and in clinical rehabilitation of visual disorders is to devise efficient training regimens that allow for the transfer, or generalization, of improvements across locations, features, and tasks. Developing perceptual expertise often takes extensive practice over a long time and is usually task-specific; thus, developing skill across a range of stimuli and tasks is typically time consuming and effortful. Even among experts, error rates in radiological interpretation remain high (Waite et al., 2019). VPL training improves visual performance in individuals with peripheral damage (Nahum, Nelken, & Ahissar, 2009); visual acuity in people with amblyopia (Levi, 2005; Levi & Li, 2009; Polat, Ma-Naim, Belkin, & Sagi, 2004; Polat, Ma-Naim, & Spierer, 2009; Xi, Jia, Feng, Lu, & Huang, 2014; Zhang, Cong, Klein, Levi, & Yu, 2014) or people with presbyopia (Polat et al., 2012; Sterkin et al., 2018); visual acuity and contrast sensitivity in people with severe optical aberrations (Barbot et al., 2017; Sabesan, Barbot & Yoon, 2017); contrast sensitivity in people with cortical blindness (Barbot et al., 2020; Cavanaugh, Barbot, Carrasco, & Huxlin, 2019; Cavanaugh, Zhang, Melnick, Das, Roberts, Tadin, Carrasco, & Huxlin, 2015; Sahraie,

Trevethan, MacLeod, Murray, Olson, & Weiskrantz, 2006; Saionz, Tadin, Melnick, & Huxlin, in press); and visual motion discrimination in people with V1 damage (Cavanaugh et al., 2019; Das, Tadin, & Huxlin, 2014; Huxlin, Martin, Kelly, Riley, Friendman, Burgin, & Hayhoe, 2009). However, prognoses for these visual disorders remain poor. A greater understanding of the factors important to and mechanisms responsible for VPL generalization is crucial for developing effective visual training and rehabilitation protocols that take full advantage of plasticity in the adult brain. Given that many vision disorders are characterized by functioning vision at some retinal locations and severe deficits at other locations, and that many perceptual skills rely on increased sensitivity to many fine features, the potential for transfer of VPL to untrained locations and features is well worth exploring.

Several studies have shown that, under certain training regimens, VPL generalizes to untrained locations (Donovan & Carrasco, 2018; Donovan, Szpiro, & Carrasco, 2015; Harris, Gliksberg, & Sagi, 2012; Hung & Seitz, 2014; Jeter et al., 2009; Wang, Zhang, Klein, Levi, & Yu, 2014; Xiao et al., 2008; Zhang, Xiao, Klein, Levi, & Yu, 2010), features (Liu, 1999; Liu & Weinshall, 2000; Sowden, Rose, & Davies, 2002; Szpiro, Spering, & Carrasco, 2014; J.-Y. Zhang et al., 2010), and tasks (Szpiro & Carrasco, 2015). Double training protocols, in which observers train at two or more locations with several stimulus features or tasks, elicit transfer of VPL, including Vernier learning, to that additional location or task (Hung & Seitz, 2014; Mastropasqua, Galliussi, Pascucci, & Turatto, 2015; Wang, Zhang, Klein, Levi, & Yu, 2012; Xiao et al. 2008; Xie & Yu, 2017). Double training studies support the general notion that interleaving multiple tasks during training promotes learning. For example, interleaving training on an orientation comparison task and a spatial frequency comparison task (i.e., observers had to compare two stimuli and indicate which stimulus was more clockwise or had a higher spatial frequency) using the same stimuli (Gabor patches) enables VPL on both tasks, whereas training on only one of the tasks is insufficient to produce learning for that task (Szpiro, Wright, & Carrasco, 2014).

Vernier hyperacuity learning can be "piggybacked" or transferred to an untrained location when paired with less location-specific orientation or motion-direction learning but does not transfer locations when training alongside a more location-specific contrast-discrimination task (Wang et al., 2014). Even so, the "piggybacking" effect appears to be limited by task design and training protocol, as double training does not elicit the transfer of hyperacuity learning when the training uses a method of constant stimuli or a single staircase, but it has been shown to elicit transfer for training with multiple short staircases in which a larger portion of trials are above

threshold (Hung & Seitz, 2014, but see Zhang & Yu, 2018, who found transfer with both short and long staircases).

Selective visual attention, which prioritizes a subset of sensory information for enhanced processing, has been assumed to play a critical role in VPL (for reviews, see Ahissar & Hochstein, 2004; Goldstone, 1998; Ito, Westheimer, & Gilbert, 1998; Li, Piech, & Gilbert, 2004; Lu et al., 2010; Roelfsema & van Ooyen, 2005; Seitz & Watanabe, 2005; Tsushima & Watanabe, 2009; Watanabe & Sasaki, 2015). However, the role of attention has often been inferred, rarely operationalized or directly manipulated, and rarely compared to a baseline condition without attention. In behavioral studies, it has been equated with task difficulty (Bartolucci & Smith, 2011; Huang & Watanabe, 2012), used interchangeably with conscious perception (Tsushima & Watanabe, 2009), and used to describe the fact that observers perform a task with a specific stimulus (Chirimuuta, Burr, & Morrone, 2007; Meuwese, Post, Scholte, & Lamme, 2013; Paffen, Verstraten, & Vidnyánszky, 2008; Seitz, Kim, & Watanabe, 2009; Watanabe & Sasaki, 2015; Watanabe et al., 2001). In neuroimaging studies, the role of attention has been inferred from neural activity in attention-related brain areas (Mukai, Kim, Fukunaga, Japee, Marrett, & Ungerleider, 2007; Tsushima, Sasaki, & Watanabe, 2006). Despite the lack of empirical studies isolating the role of attention in VPL, several papers have relied on hypotheses regarding the role of attention either as a gating mechanism for enabling VPL (Ahissar & Hochstein, 2004; Roefsema & van Ooyen, 2005; Roelfsema, van Ooyen, & Watanabe, 2010; Sasaki, Nañez, & Watanabe, 2010) or as having important implications for the emergence of transfer versus specificity of VPL (Fahle, 2009; Mukai et al., 2007; Sasaki, Nañez, & Watanabe, 2012; Wang et al., 2014; Watanabe & Sasaki, 2015; Yotsumoto & Watanabe, 2008; T. Zhang et al., 2010; Zhang et al., 2013).

Visual attention can be covertly deployed (i.e., without accompanying eye movements) in a voluntary, goal-driven manner (endogenous attention) or in an involuntary, stimulus-driven fashion (exogenous attention). Both endogenous attention and exogenous attention improve performance on a variety of tasks mediated by early visual processes (for reviews, see Carrasco, 2011; Carrasco, 2014; Carrasco & Barbot, 2015; Maunsell, 2015). Because attention serves as one of the most important mechanisms for gating what and how efficiently information is processed, a greater understanding of VPL requires an understanding of how attention modulates it. Nonetheless, very few studies have directly manipulated attention to examine its effect. It has been reported that the effects of object-based attention decrease with training (Dosher, Han, & Lu, 2010) and feature-based attention facilitates recovery of motion perception in people with cortical blindness (Cavanaugh et al., 2019).

Particularly relevant for the present studies are four studies in which covert spatial attention was manipulated (Donovan & Carrasco, 2018; Donovan et al., 2015; Mukai, Bahadur, Kesavabhotla, & Ungerleider, 2011; Szpiro & Carrasco, 2015). One study manipulated covert spatial attention but did not isolate the attentional cueing effect on learning because observers learned using all cue validity types (valid, neutral, and invalid) (Mukai et al., 2011). To isolate the attentional effect, the other three studies trained separate groups of observers on either valid or neutral cues only. Szpiro and Carrasco (2015) trained observers with exogenous attention, using peripheral cues, and found that those observers learned, whereas those who trained with neutral cues under otherwise identical conditions showed no such learning. Interestingly, exogenous attention also enabled learning for an untrained task that used the same stimulus but not for an orthogonal stimulus in either the trained or untrained task; thus, there was task transfer but not feature transfer. Two other studies from our lab found that deploying exogenous (Donovan et al., 2015) or endogenous (Donovan & Carrasco, 2018) spatial attention during training facilitated the transfer of improved orientation discrimination performance to untrained locations via response gain and contrast gain, respectively. Importantly, these studies manipulated whether attention was deployed to the trained locations via a valid cue or distributed via a neutral cue only during training. Observers from both groups were tested with neutral cues before and after training, such that evidence of location transfer was only attributable to attentional allocation during training.

Exogenous attention also improves performance in acuity tasks (Anton-Erxleben & Carrasco, 2013; Carrasco & Barbot, 2015). To date, there have been no studies that directly manipulate spatial attention on VPL in acuity tasks and no studies designed to assess the potential modulation by attention of feature specificity. We adapted our earlier protocol to investigate exogenous spatial attention's influence on location specificity in an orientation discrimination task (Donovan et al., 2015) to two acuity tasks: Landolt square gap discrimination (Experiment 1) and Vernier Gabor misalignment discrimination (Experiment 2). Given that exogenous attention has been shown to improve performance in Landolt square acuity tasks (Carrasco, Williams, & Yeshurun, 2002; Golla, Ignashchenkova, Haarmeier, & Thier, 2004; Montagna, Pestilli, & Carrasco, 2009; Yeshurun & Carrasco, 1999) and to increase apparent gap size (Gobell & Carrasco, 2005), we investigated whether the same mechanism facilitates transfer to untrained locations in Experiment 1. Given that both exogenous attention (Yeshurun & Carrasco, 1999) and VPL (Saarinen & Levi, 1995; Sotiropoulos et al., 2011) have been separately shown

to decrease Vernier discrimination threshold, in Experiment 2 we assessed whether exogenous attention could transfer learning to untrained retinotopic locations and to untrained orthogonal orientations in the location- and feature-specific Vernier hyperacuity task. Similar to the logic of our previous studies, here we only manipulated the type of cue used during training in an otherwise identical VPL task procedure. Half of the observers trained with exogenous attention (attention group) and half trained with neutral distributed attention (neutral group). Doing so allows us to effectively isolate the influence of exogenous spatial attention on learning specificity in acuity tasks.

In this study, we were particularly interested in investigating the effects of exogenous attention, a selective mechanism corresponding to the automatic and transient capture of attention at the cued location (e.g., Pestilli & Carrasco, 2005; Yeshurun & Carrasco, 1998), given its potential to enhance visual improvements and generalization, with no additional time or effort. Note that during the pre- and post-test sessions, as well as during the training sessions, observers already know stimulus locations and features they have to discriminate. Thus, in principle, observers in both the neutral and attention groups could attend to such attributes. For that reason, any differential effect between groups in learning acquisition in the trained condition, as well as in its specificity (lower performance in the untrained locations and features relative to the trained location and feature condition), could only be due to exogenous attention, under which observers trained in the attention group but not in the neutral group.

Experiment 1

Methods

Observers

All 26 observers (19 females; $M = 24.9$ years old; range, 18–35) had normal or corrected-to-normal vision, were naïve to the purposes of this study, and had no previous experience with the Landolt square gap discrimination. The experiment was conducted with informed consent obtained from each observer. The University Committee on Activities involving Human Subjects at New York University approved the experimental protocols, and all research was performed in accordance with relevant guidelines and regulations.

Apparatus

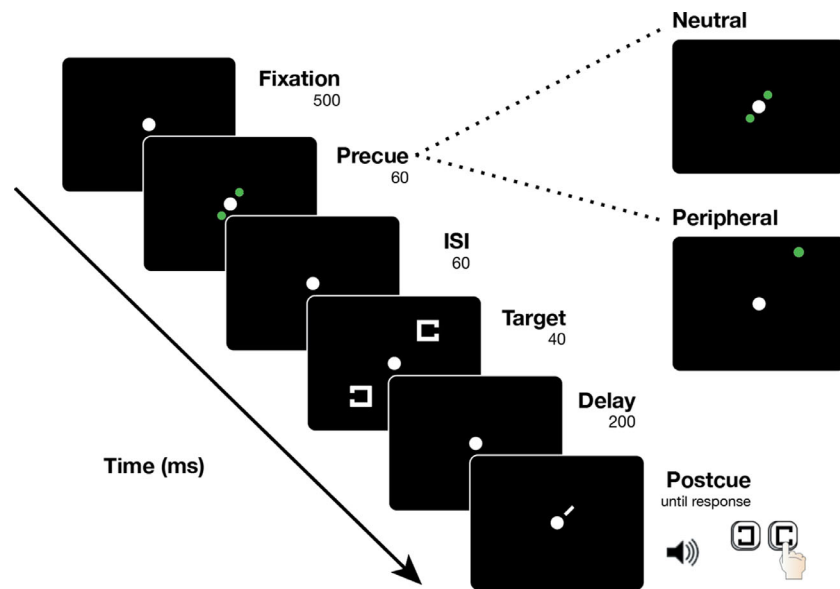Stimuli were generated using Psychtoolbox (Brainard, 1997; Pelli, 1997) in MATLAB (MathWorks,

Figure 1. Trial sequence for Experiment 1. Observers fixated on a circle at the center of the screen. A precue presented for 60 ms was either two green circles near the center (neutral) or one green dot above the upcoming target locations (valid and peripheral). After a brief ISI, two Landolt squares were presented for 40 ms along one diagonal (top left and bottom right, or top right and bottom left). After a 200-ms delay, a postcue appeared indicating the target Landolt square. Observers had to report which side of the target the gap was on. Auditory feedback was provided after each trial.

Natick, MA) and were displayed on a 21-in. cathode-ray tube monitor (1280 × 960 at 85 Hz). Eye position was monitored using an infrared eye tracker (Eyelink 1000 CL; SR Research, Kanata, Ontario, Canada). Observers viewed the screen from 114 cm away, using a chin rest to stabilize head position.

Stimuli and procedure

Stimuli were presented on a black background. Figure 1 illustrates the trial sequence. Each trial began with a white fixation circle (subtending 1.5 degrees of visual angle [dva]) presented at the center of the screen. The fixation circle remained on the screen for the rest of the trial. After 500 ms of only the fixation point on the screen, a precue appeared for 60 ms. The precue was either neutral and central (two green dots, subtending 0.1°, 0.7° from fixation, and in intercardinal positions along one diagonal) or valid and peripheral (green circle subtending 0.2° presented 0.95° above the upcoming target). Following a 40-ms interstimulus interval (ISI), two Landolt squares appeared for 60 ms along one diagonal (top left and bottom right, or top right and bottom left), 7.5° from center fixation, corresponding to the locations indicated by the neutral precue. The Landolt squares (outline squares 1° × 1°) had seven gap sizes, equally likely, chosen randomly from trial to trial (method of constant stimuli), and ranging from 0.0625° to 0.5°. The two Landolt square stimuli always had equivalent gap sizes, and the side of each stimulus that

contained the gap was randomly and independently generated for each Landolt square on a given trial. Following a 100-ms delay, a postcue (a short 0.42° diagonal white line) appeared at fixation, indicating which of the two stimulus locations was the target. The postcue always indicated the same location as the precue if the precue was peripheral (precue 100% valid) or one of the two diagonal locations if the precue was neutral. Observers were required to indicate, using key presses, whether the gap occurred on the left or right side of the Landolt square at the location indicated by the postcue. Auditory feedback was provided after each trial informing observers of the accuracy of their response, and text feedback was provided at the end of each block informing observers of their percent correct on that block.

To initiate a trial, observers were required to fixate at the center and maintain fixation until the response window. Stimulus presentation was contingent on maintaining fixation. If observers broke fixation at any point (1.5° from fixation) before the response window, the trial would end immediately, and a trial with identical parameters (stimuli and target locations, gap location and size) would be added to the end of the block, ensuring successful completion of all trials within the block without an eye movement.

Figure 2 shows the training schedule. Before the first session (the pre-test), all observers completed 30 trials of a practice task in which a white line oriented left or right was presented left or right of fixation. The
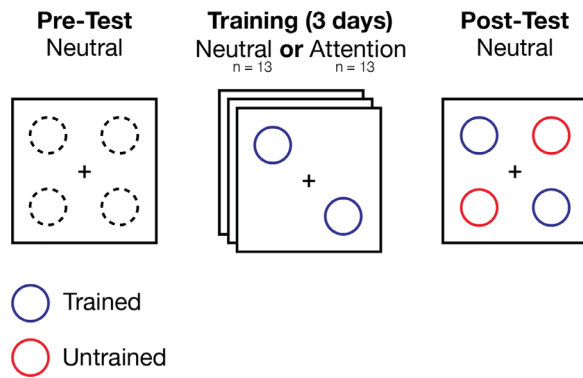
Figure 2. Training and testing schedule for Experiment 1. Observers were tested at four locations, one diagonal per block of trials, before and after 3 days of training at two locations along one diagonal. This meant that, for each observer, there were two trained locations along one diagonal and two untrained locations along the other diagonal. Half of the observers were trained with all valid cues (attention training group), and half with neutral cues (neutral training group). All observers received only neutral cues on pre- and post-tests.

practice task had the same procedure and timing as the experiment but with different stimuli (oriented lines) presented at different locations from those used in the main experiment. The purpose of the practice was to familiarize observers with the procedure and to reduce procedural learning during experimental blocks.

The pre-test consisted of 10 blocks of 112 trials per block. Within a single block, two Landolt squares appeared along the one diagonal (i.e., top left and bottom right in one block, top right and bottom left in another). Each trial, the target stimulus, or the Landolt square that observers reported on as indicated by the postcue, was randomly chosen as one of the two Landolt squares. The tested diagonal alternated between blocks. All trials in the pre-test had a neutral cue. Post-tests were identical in structure to pre-tests except that they were administered after the training sessions. The pre-test and the post-test were identical for all observers. The middle three sessions were training sessions. Observers were randomly assigned to the neutral or the attention group. Half of the observers ($n = 13$) were in the neutral training group, in which the neutral precue appeared on all trials. The other half of the observers were in the attention training group, in which a valid peripheral precue appeared above the target location on all trials. All observers were trained with stimuli appearing along the same diagonal for all blocks, and the postcue randomly indicated either location as the target. The trained diagonal was counterbalanced across observers (i.e., only top left or bottom right for one observer, only top right or bottom left for another). Thus, each observer had two trained locations, and the two locations in the other diagonal were untrained.

The five sessions of Experiment 1 occurred on 5 consecutive days. The pre-test occurred on day 1 and the post-test on day 5, and training took place from day 2 to 4.

Analysis

For each observer and for each of the five sessions, we computed accuracy as a function of gap size and fitted the data with Weibull functions to estimate 75%-correct gap-size thresholds for each diagonal (trained vs. untrained). We averaged the thresholds within each condition on each session and assessed how the change in thresholds after training differed between the neutral and attention groups. We assessed the effects of training (within-subject) and attention (between subject) on Landolt square gap-size thresholds using an ANOVA and verified our results using a Bayesian analysis (Masson, 2011).

Results

We investigated whether and how performance changed between the pre- and the post-tests at the trained locations compared to performance at the untrained locations. To do so, we compared the threshold value, defined as the gap size required to be 75% accurate, between (1) the pre- and post-test, and (2) the trained and untrained locations. Performance at the two trained locations was analyzed collectively within each session, and the same was done for the two untrained locations.

We performed a three-way mixed ANOVA using threshold values, where the within-subjects factors were location (trained vs. untrained) and training (pre-test vs. post-test), and the between-subjects factor was group (neutral vs. attention) (Figure 3). There was a main effect of training, $F(1,24) = 38.848$, $P < 0.001$, and $\eta_p^2 = 0.618$, indicating that the threshold was different between the pre-test and the post-test. No other factors or interactions were significant, including the three-way interaction among location, training, and cue type (all $P > 0.1$). We performed a paired-samples t-test between pre-test and post-test thresholds. For trained and untrained locations, in both attention and neutral groups all pairwise comparisons were significant ($P < 0.05$). These results indicate that learning, assessed by a lower threshold value at the post-test compared to the pre-test, was not different at trained and untrained locations between the attention and neutral groups.

We performed two separate two-way ANOVAs between location and training, within the neutral group only and the attention group only, to assess if there was any difference in learning at trained and untrained locations. The interaction was not significant in either group: neutral, $F(1,12) = 2.16$ and $P > 0.1$; attention,
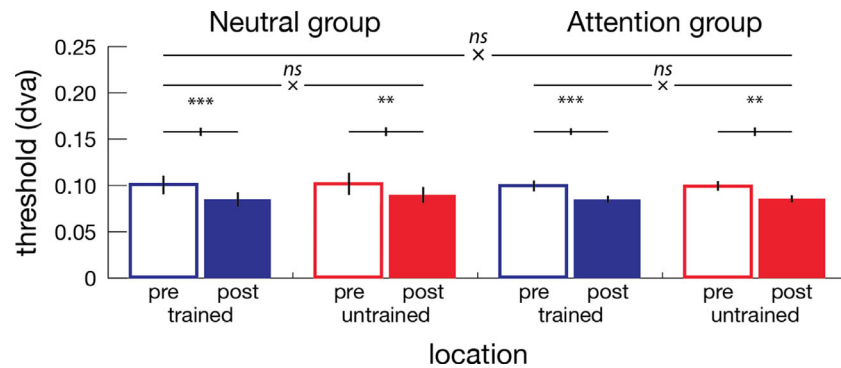
Figure 3. Results for Experiment 1. We compared Landolt square gap-discrimination thresholds (in dva) between pre-test and post-test, at trained and untrained locations, and between the neutral and attention groups. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Error bars are ± 1 *SEM*.

$F(1,12) < 1$. This indicates that for both groups the extent of learning was comparable between the trained and untrained locations.

These results were confirmed by a Bayesian model selection analysis (Masson, 2011). We transformed the sum of squared errors obtained from our ANOVAs to arrive at an estimated Bayes factor as well as Bayesian information criterion probabilities (*p*BIC) for the alternative (H$_1$) hypotheses given dataset D. Here, we report the probability of the alternative hypotheses—*p*BIC(H$_1$|D)—which shows positive evidence for the alternative hypothesis above 0.75 and positive evidence for the null hypothesis below 0.25. In between those values, the evidence is inconclusive (Masson, 2011; Raftery, 1995). This analysis showed positive evidence for the alternative hypothesis for the main effect of training: *p*BIC(H$_1$|D) = 0.999 for the three-way mixed ANOVA, *p*BIC(H$_1$|D) = 0.976 for the two-way ANOVA in the neutral group, and *p*BIC(H$_1$|D) = 0.999 for the two-way ANOVA in the attention group. All other factors and interactions in the three-way mixed ANOVA showed positive evidence for the null hypothesis (no effect): location, *p*BIC(H$_1$|D) = 0.048; location × cue type, *p*BIC(H$_1$|D) = 0.046; training × cue type, *p*BIC(H$_1$|D) = 0.037; location × training, *p*BIC(H$_1$|D) = 0.069; and location × training × cue type, *p*BIC(H$_1$|D) = 0.039. In the two-way ANOVAs, this analysis indicated inconclusive results for the interaction between location and training in the neutral group, *p*BIC(H$_1$|D) = 0.448, and positive evidence for the null hypothesis for the attention group, *p*BIC(H$_1$|D) = 0.237. For the main effect of location, results were inconclusive for the neutral group, *p*BIC(H$_1$|D) = 0.306, but there was positive evidence for the null hypothesis for the attention group, *p*BIC(H$_1$|D) = 0.217.

We analyzed reaction time (RT) as a secondary measure to rule out any speed-accuracy trade-off. We performed a three-way mixed ANOVA on the geometric means of RT for each location and session. There was a main effect of training, $F(1,24) = 21.493$ and $P = 0.001$,

indicating that RT similarly improved with training. No other factors or interactions were significant ($P > 0.1$). These results indicate that there was no speed–accuracy trade-off, as observers were faster at the post-test when threshold values were lower. In sum, both groups had significant learning at the trained location and transferred learning to the untrained location.

Experiment 2

Methods

Observers

Thirty-two observers completed this experiment (23 females; $M = 23.4$ years old; range, 18–31). All observers had normal or corrected-to-normal vision, were naïve to the purposes of this study, and had no previous experience with the Vernier hyperacuity task. The experiment was conducted with informed consent obtained from each observer. The University Committee on Activities Involving Human Subjects at New York University approved the experimental protocols, and all research was performed in accordance with relevant guidelines and regulations.

Apparatus

The apparatus was the same as in Experiment 1. The only difference was that observers viewed the screen from 57 cm away and at 100 Hz, using a chin rest to stabilize head position.

Stimuli and procedure

Stimuli were presented on a gray background. Figure 4 shows the trial sequence. Each trial began with the presentation of a white fixation cross (0.4° × 0.4°) at the center of the screen. The fixation-cross remained
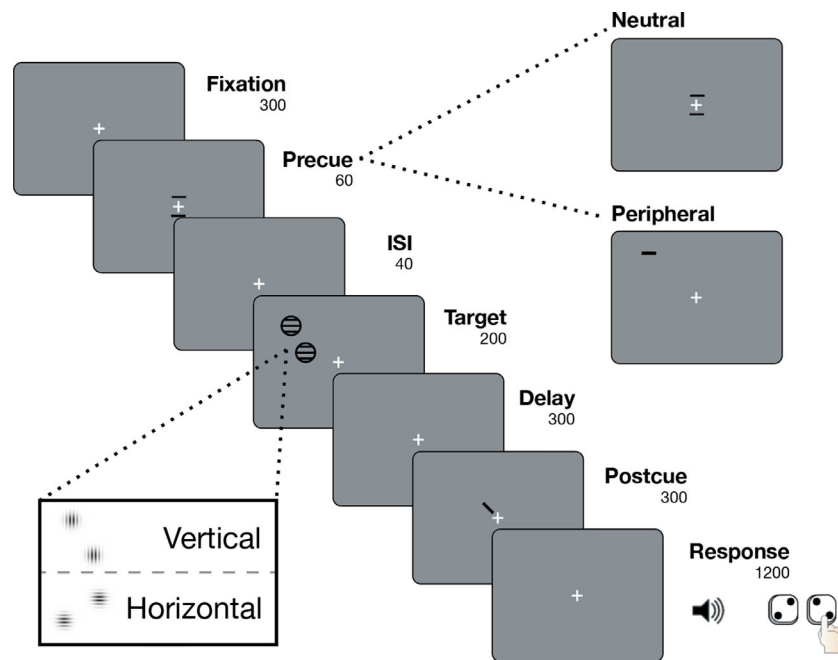
Figure 4. Trial sequence for Experiment 2. Observers fixated on a central cross. A precue was presented for 60 ms and was either two lines above and below the fixation cross (neutral) or one line above the upcoming target (valid and peripheral). After a brief ISI, two Gabor patches were presented at one of four possible intercardinal locations and were either horizontally or vertically offset. After a 300-ms delay, a postcue appeared for 300 ms, indicating the location at which the target appeared. Observers were given 1200 ms to report whether the right Gabor patch was higher or lower than the left Gabor patch (horizontal orientation) or whether the bottom Gabor patch was left or right relative to the top Gabor patch (vertical orientation). Auditory feedback was provided after each trial.

on the screen for the duration of each trial. After 300 ms of only the fixation cross on the screen, a precue appeared for 60 ms. The precue was either neutral and central (two 0.2° × 0.1° black lines 0.9° above and below the fixation cross) or valid and peripheral (one 0.4° × 0.1° black line 2.55° above the upcoming target if the target was in the upper visual field and below the upcoming target if the target was in the lower visual field). After a 40-ms ISI, two Gabor patches (5 cpd, at 80% contrast, each subtending 1° and 1° apart) were presented for 200 ms at one of four intercardinal isoeccentric locations 5° from fixation. The Gabor patches were horizontally (horizontal orientation) or vertically (vertical orientation) aligned, ranging from 0.01° to 0.1° horizontal or vertical offset, respectively. The offset distance between the Gabor patches followed a staircase (psi-method) with a performance criterion of 75% for each block. Following a 300-ms delay, to eliminate location uncertainty, a postcue (black line, 0.75° in length) was presented 0.65° from fixation for 300 ms, pointing toward the location where the target had just been presented. A brief tone then indicated the initiation of a 1200-ms window during which observers could give their responses. Observers were required to indicate, using key presses, whether the right Gabor patch was higher or lower than the left Gabor patch (horizontal orientation) or whether the bottom Gabor

patch was left or right relative to the top Gabor patch (vertical orientation). Auditory feedback was provided after each trial informing observers of the accuracy of their response, and text feedback was provided at the end of each block informing observers of their percent correct for that block.

To initiate a trial, observers were required to fixate at the center of the cross and maintain fixation, without blinking, until the onset of the response window. Stimulus presentation was contingent on maintaining fixation. If observers broke fixation at any point (2° from the center of the cross) before the response window, the trial would end immediately, and a trial with identical parameters (stimulus location, orientation, and offset) would be added to the end of the block, ensuring successful completion of all trials within the block without an eye movement.

Figure 5 shows the training schedule. As in Experiment 1, the five sessions occurred on 5 consecutive days. The pre-test occurred on day 1 and the post-test on day 5, and training took place from day 2 to day 4. Before the first session (the pre-test), all observers completed 20 trials of practice with red and blue circles appearing at peripheral locations used during the full experiment and with neutral cues. This was meant to familiarize these inexperienced observers with performing a psychophysics task, and
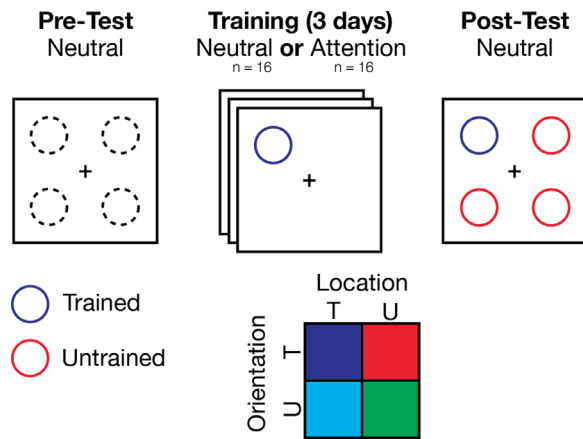
Figure 5. Training and testing schedule for Experiment 2. Observers were tested at four locations, one per block of trials, before and after 3 days of training at one of the four locations. Each observer trained at one location for one orientation (horizontal or vertical) only. This meant that, for each observer, there were four stimulus conditions at the post-test: trained location + trained orientation, trained location + untrained orientation, untrained location + trained orientation, and untrained location + untrained orientation. Half of the observers were trained with all valid peripheral cues (attention training group) and half with neutral cues (neutral training group). All observers received only neutral cues on pre- and post-tests.

afterward they performed 40 to 60 trials of the Vernier discrimination task in a separate set of practice blocks in order to reduce procedural learning during experimental blocks. The pre-test (day 1) consisted of 24 blocks of 50 trials each (12 blocks with vertical orientation and 12 blocks with horizontal orientation, with the order of the tested orientation counterbalanced between observers). The location of the target (top left, top right, bottom left, or bottom right) varied among blocks, such that each location was assessed three times in three separate blocks, in random order. There were short breaks between blocks and halfway through each block (after 25 trials). A neutral precue was presented on each trial. The post-test (day 5) was identical in structure to the pre-test.

The next three sessions (days 2–4) after the pre-test were training sessions, in which 12 blocks of 50 trials each were completed per session. For each observer, in all 12 blocks in all three training sessions, stimuli were in either the horizontal orientation or the vertical orientation and appeared at only one location (top left, top right, bottom left, or bottom right), such that the other three locations were untrained. During training, half of the observers (n = 16) trained with valid peripheral precues adjacent to the target location on all trials (attention group) and half of the observers trained with neutral precues on all trials (neutral group). Observers were randomly assigned to the neutral or the attention group. For each observer in both training

groups, there were four possible conditions: trained location + trained orientation, trained location + untrained orientation, untrained location + trained orientation, and untrained location + untrained orientation.

Analysis

For each observer and on each of the five sessions, we calculated their gap threshold using a psi-method staircase, converging on 75% accuracy threshold on each block. We averaged the thresholds within each condition on each session and assessed how the change in thresholds after training differed between the neutral and attention groups. We assessed location and feature specificity in separate ANOVAs and verified our results with a Bayesian analysis, as in Experiment 1.

Results

We investigated whether and how performance differed between pre-tests and post-test, defining learning as a lower Gabor misalignment threshold (in dva) at the post-test. We took the mean performance at all three untrained locations to compare with performance at the trained location. We compared the pre-test and post-test thresholds (1) at the trained versus untrained locations for the trained orientation, and (2) for the trained versus untrained orientations at the trained location.

Learning at trained and untrained locations

To assess learning at trained and untrained locations, a three-way mixed ANOVA, with within-subjects factors of location (trained vs. untrained) and training (pre-test vs. post-test) and a between-subjects factor of group (neutral or attention), was conducted using threshold values for the trained orientation only. In other words, we compared performance only for the trials in which observers were presented with the same orientation they had encountered during training (Figure 6). This allowed us to isolate location learning. We found a main effect of training, $F(1,30) = 23.941$, $P < 0.001$, and $\eta_p^2 = 0.444$, indicating performance was better at post-test than at pre-test, or learning. There was a significant interaction between location and training: $F(1,30) = 5.051$, $P < 0.05$, and $\eta_p^2 = 0.144$. To understand this significant interaction between location and training, we performed the same ANOVA but within only the neutral group and within only the attention group. For both groups, there were again main effects of training: neutral group,: $F(1,15) = 18.884$, $P < 0.01$, and $\eta_p^2 = 0.557$; attention group, $F(1,15) = 7.994$, $P < 0.05$, and $\eta_p^2 = 0.348$. For the neutral group, there was a marginally significant interaction
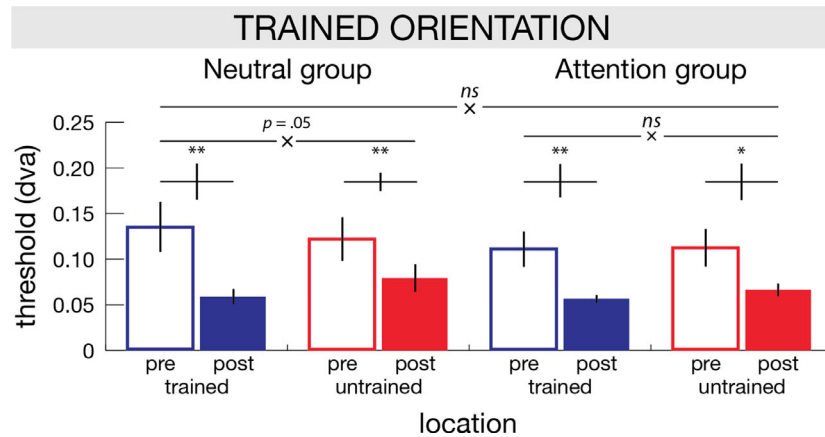
Figure 6. Results for the trained orientation only in Experiment 2. We compared Gabor misalignment thresholds (in dva) between pre-test and post-test, at trained and untrained locations, and between the neutral and the attention groups. $^*P < 0.05$; $^{**}P < 0.01$. Error bars are ± 1 *SEM*.

between location and training, $F(1,15) = 4.339$, $P = 0.055$, and $\eta_p^2 = 0.224$, due to greater learning at the trained than at the untrained location. Importantly, this interaction was not found in the attention group ($P > 0.05$), indicating that learning was not different between trained and untrained locations.

These results were confirmed by a Bayesian model selection approach (Masson, 2011). In the three-way mixed ANOVA, we found positive evidence for the alternative hypothesis for the main effect of training, $p\text{BIC}(\text{H}_1|\text{D}) = 0.997$, and inconclusive evidence for the interaction between location and training, $p\text{BIC}(\text{H}_1|\text{D}) = 0.273$. For the ANOVA in the neutral group, we found positive evidence for the alternative hypothesis for the main effect of training, $p\text{BIC}(\text{H}_1|\text{D}) = 0.994$, and inconclusive evidence for the interaction between training and location, $p\text{BIC}(\text{H}_1|\text{D}) = 0.655$. For the ANOVA in the attention group, we found positive evidence for the alternative hypothesis for the main effect of training, $p\text{BIC}(\text{H}_1|\text{D}) = 0.885$, and inconclusive evidence for the interaction between training and location, $p\text{BIC}(\text{H}_1|\text{D}) = 0.275$.

The marginal significance between location and training in the neutral group led us to consider the possibility of partial transfer of learning to the untrained location. To further explore, we bootstrapped the three-way ANOVA for both experimental groups over 1000 iterations using bootstrapped data that was also over 1000 iterations. Of the bootstrapped ANOVAs, the interaction between location and training was significant around 292 times in the neutral group ($P < 0.05$), supporting the notion of some transfer to the untrained location. In contrast, the interaction between location and training was significant only 30 out of 1000 times in the attention group ($P < 0.05$), which shows reliable complete transfer of learning to the untrained location.

Finally, we analyzed RT as a secondary measure to rule out any speed–accuracy trade-off. Unlike in

Experiment 1, in Experiment 2 observers waited for the response cue before giving their response within a 1200-ms time window. For that reason, we hypothesized no difference in RTs between conditions. For the trained location, we performed a three-way mixed ANOVA on RT, with within-subjects factors of orientation (trained vs. untrained) and training (pre-test vs. post-test) and a between-subjects factor of group (neutral or attention), and found a significant main effect of training: $F(1,30) = 5.726$, and $P < 0.05$. No other factors or interactions were insignificant (all $P > 0.1$). These results indicate that there is no speed–accuracy trade-off.

Learning for trained and untrained orientations

To isolate feature learning, we compared performance only at the trained location (Figure 7). We conducted a three-way mixed ANOVA, with within-subjects factors of orientation (trained vs. untrained) and training (pre-test vs. post-test) and a between-subjects factor of group (neutral vs. attention), to assess learning for trained and untrained orientations at the trained location only. We found a significant main effect of training, $F(1,30) = 17.792$, $P < 0.001$, and $\eta_p^2 = 0.372$, indicating that learning was different between trained and untrained orientations. There was a significant three-way interaction among orientation, training, and group, $F(1,30) = 4.713$, $P < 0.05$, and $\eta_p^2 = 0.136$, as well as two marginal significant interactions between orientation and group, $F(1,30) = 3.906$, $P = 0.057$, and $\eta_p^2 = 0.115$, and between orientation and training: $F(1,30) = 3.732$, $P = 0.063$, and $\eta_p^2 = 0.111$. To understand these interactions, we conducted two-way ANOVAs between orientation and training for only the neutral group and only the attention group. They both revealed a main effect of training: neutral group, $F(1,15) = 10.535$, $P < 0.01$, and $\eta_p^2 = 0.413$; attention group, $F(1,15) = 8.101$, $P < 0.05$, and η_p^2
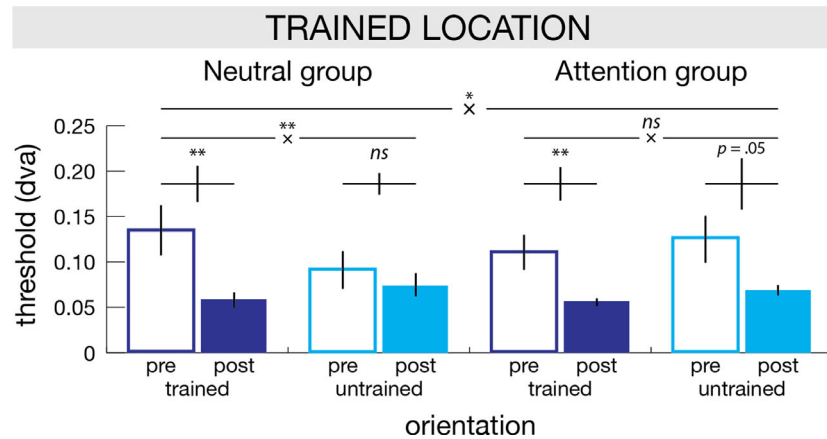
Figure 7. Results at the trained location only in Experiment 2. We compared Gabor misalignment thresholds (in dva) between pre-test and post-test, at trained and untrained orientation, and between the neutral and the attention groups. $^*P < 0.05$; $^{**}P < 0.01$. Error bars are ± 1 *SEM*.

$= 0.351$. In the neutral group, there was a significant interaction between orientation and training, $F(1,15) = 16.076$, $P < 0.05$, and $\eta_p^2 = 0.517$, indicating that there was more learning for the trained than the untrained orientation. There was no corresponding interaction in the attention group ($P > 0.1$), which reveals that learning was comparable for the trained and the untrained orientation.

A Bayesian model selection analysis confirmed our results. In the three-way mixed ANOVA, we found positive evidence for the alternative hypothesis for the main effect of training, $p\mathrm{BIC}(\mathrm{H_1|D}) = 0.982$, and inconclusive evidence for the three-way interaction among orientation, training, and group, $p\mathrm{BIC}(\mathrm{H_1|D}) = 0.245$. We found positive evidence for the null hypothesis (no effect) for the interactions between orientation and group and between orientation and training, $p\mathrm{BIC}(\mathrm{H_1|D}) = 0.181$ and 0.170, respectively. In the two-way ANOVA in the neutral group, we found positive evidence for the alternative hypothesis for the main effect of training, $p\mathrm{BIC}(\mathrm{H_1|D}) = 0.947$, and for the interaction between training and orientation, $p\mathrm{BIC}(\mathrm{H_1|D}) = 0.988$. In the attention group, we found positive evidence for the alternative hypothesis for the main effect of training, $p\mathrm{BIC}(\mathrm{H_1|D}) = 0.888$, and positive evidence for the null hypothesis (no effect) for the interaction between training and orientation, $p\mathrm{BIC}(\mathrm{H_1|D}) = 0.201$.

RT analysis for the trained orientation showed a significant interaction among location, training, and group, $F(1,30) = 4.230$, $P < 0.05$. No other factors or interactions were significant ($P > 0.1$). Two-way ANOVAs within each group, with within-subjects factors of location (trained vs. untrained) and training (pre-test vs. post-test), revealed no significant factors or interactions ($P > 0.1$). These results indicate that there is no speed–accuracy trade-off.

Finally, we performed paired-samples *t*-tests for each pair of pre-test and post-test threshold, for trained and untrained locations and orientations, in the attention group and the neutral group. Consistent with the main effects of training in the ANOVAs above, all but one pairwise comparison were significant. The nonsignificant pairwise comparison ($P > 0.1$) was for the untrained orientation at the trained location in the neutral group, indicating that performance did not improve for the untrained orientation when its location was not cued. Otherwise, observers had significantly lower post-test thresholds at all locations and orientations and with both neutral and valid peripheral cues.

Learning at the untrained location and for the untrained orientation

For exploratory reasons, we also assessed learning for the untrained orientation at the untrained location. We performed a paired-samples *t*-test for pre- and post-test thresholds in the attention group and the neutral group for this condition. We found a significant difference in the neutral group ($t = 2.191$, $P < 0.05$), but not in the attention group ($P > 0.05$). This finding reveals concurrent feature and location transfer when training with the valid peripheral cue, but feature and location specificity when training with the neutral cue.

Using the difference in threshold between the pre- and post-tests, we conducted a three-way mixed ANOVA, with within-subjects factors of location (trained vs. untrained) and orientation (trained vs. untrained) and a between-subjects factor of group (neutral or attention). We found a significant three-way interaction among location, orientation, and group, $F(1,30) = 6.281$, $P < 0.05$, and $\eta_p^2 = 0.173$, indicating
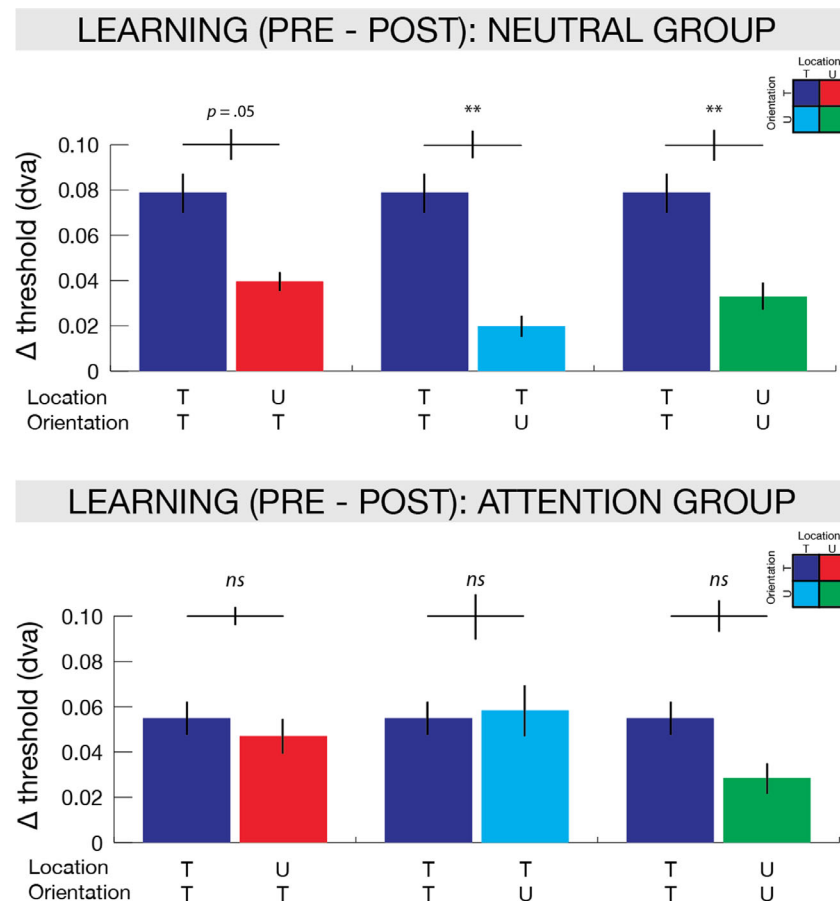
Figure 8. Results comparing the change in Gabor misalignment thresholds (in dva) between pre-test and post-test, at trained and untrained locations with trained and untrained orientation, between the neutral and the attention groups. $^*P < 0.05$; $^{**}P < 0.01$. Error bars are ± 1 *SEM*.

that the neutral and attention groups differed in feature and location transfer (Figure 8). We found a significant main effect of location, $F(1,30) = 5.273$, $P < 0.05$, and $\eta_p^2 = 0.149$, and marginally significant main effect of orientation, $F(1,30) = 3.877$, $P = 0.058$, and $\eta_p^2 = 0.114$, indicating that learning for location and for orientation differed between groups. No other factors or interactions were significant ($P > 0.1$). In the neutral group, we found a significant main effect of orientation, $F(1,15) = 14.972$, $P < 0.01$, and $\eta_p^2 = 0.500$, and a significant interaction between location and orientation, $F(1,15) = 6.035$, $P < 0.05$, and $\eta_p^2 = 0.287$. In the attention group, there was a significant main effect of location, $F(1,15) = 4.933$, $P < 0.05$, $\eta_p^2 = 0.247$, but no effect of orientation and no interaction between location and orientation ($P > 0.1$).

The Bayesian model selection analysis confirmed our results. We found inconclusive evidence for the three-way interaction among location, orientation, and group, $p\text{BIC}(H_1|D) = 0.395$, and for the main effect of location, $p\text{BIC}(H_1|D) = 0.292$. We found positive evidence in favor of the null hypothesis (no effect) for orientation, $p\text{BIC}(H_1|D) = 0.178$. In the neutral

group, we found positive evidence for the alternative hypothesis for orientation, $p\text{BIC}(H_1|D) = 0.984$; inconclusive evidence for location, $p\text{BIC}(H_1|D) = 0.316$; and positive evidence for the interaction between location and orientation, $p\text{BIC}(H_1|D) = 0.789$. In the attention group, we found inconclusive evidence for location, $p\text{BIC}(H_1|D) = 0.708$; positive evidence for the null hypothesis (no effect) for orientation, $p\text{BIC}(H_1|D) = 0.211$; and inconclusive evidence for the interaction between location and orientation, $p\text{BIC}(H_1|D) = 0.313$.

In sum, we found partial location transfer in the neutral group and complete location transfer in the attention group, as well as feature specificity in the neutral group and feature transfer in the attention group.

Discussion

We isolated the effects of exogenous spatial attention on VPL in visual acuity. In Experiment 1, we found that observers in the neutral group and in the attention group improved similarly at both trained

and untrained locations. Unexpectedly, we did not find location specificity in the neutral condition. In this case, training with attention cues did not promote further transfer than already observed in the neutral group. In Experiment 2, for the neutral group, we found partial location transfer (some learning at the untrained location but not as much as at the trained location) and feature specificity (no learning for the untrained orientation). These results are consistent with previous studies of Vernier learning that, like our neutral condition, were performed under uncued or distributed attention, for which specificity regarding location, feature and eye was found (Fahle, 2004; Fahle & Edelman, 1993; Fahle et al., 1995). Notwithstanding such specificity, we found that training with valid, peripheral cues facilitates location transfer in the Vernier hyperacuity task, in which discrimination depends on fine spatial resolution. This extends our previous finding that exogenous attention can facilitate location transfer in an orientation-discrimination task (Donovan et al., 2015) to a task reported to be specific (Fahle, 2004; Fahle & Edelman, 1993; Fahle & Morgan, 1996; Fiorentini & Berardi, 1980; Poggio et al., 1992; see reviews by Sagi, 2011; Watanabe & Sasaki, 2015).

Another novel finding of this study is that exogenous spatial attention can also transfer learning of a stimulus orientation to an untrained, orthogonal orientation. Moreover, exogenous attention can induce transfer along two stimulus dimensions—feature and space—within the same training regime, highlighting the great potential of attentional manipulations to generalize learning. Some studies have shown feature transfer under certain conditions, often in the form of a complete lack of feature transfer to begin with (e.g., Liu, 1999; Sowden et al., 2002) or feature transfer after training on multiple tasks (e.g., J.-Y. Zhang et al., 2010). Here, we show that training on a single task that exhibits feature specificity in a distributed attention condition will exhibit feature transfer when training includes valid exogenous spatial precues while training on only one task at one location with one stimulus feature value.

The fact that feature transfer is also facilitated by exogenous attention may be surprising, considering that this bottom-up cue provided no feature information. We have speculated in the past (Donovan & Carrasco, 2018; Donovan et al., 2015) that the short-term improvement of sensory signals due to attention may enable a higher level learning mechanism to dominate, but only in the attention group—similar to the reverse hierarchy theory (RHT) (Ahissar & Hochstein, 2004). We note, however, that our study was not designed to directly test the predictions of RHT and does not provide a proof of such theory, but we speculate that our findings are consistent with it. This theory predicts specificity in difficult tasks that require high precision as long as the quality of sensory perception is a major constraint

on performance, in which case learning benefits from improving sensory processing in location- and feature-selective sensory regions of the brain. If a task is made less precise or sensory processing is enhanced, then learning may rely more on higher level regions and thus transfer is more likely. Accordingly, both a low-level and a high-level mechanism can account for threshold improvements in the trained conditions, but the latter is associated with greater transfer to untrained conditions.

Covert attention enhances low-level visual perception across many dimensions (e.g., Carrasco, 2011; Carrasco & Barbot, 2015), and in the current study it is possible that, in the attention group, exogenous attention enhanced perception sufficiently for high-level learning to dominate. Without exogenous attention, the neutral group would have relied more on a lower level mechanism that enhances sensory signals, such that the trained conditions show greater learning than the untrained conditions. Notably, this explanation could account for both location and feature transfer due to attention, as these high-level decision regions are, compared to early sensory regions, less selective for both locations and basic visual features. VPL reflects plasticity in a complex set of brain networks and may occur at multiple levels (for reviews, see Dosher & Lu, 2017; Maniglia & Seitz, 2018). Models of VPL propose that learning modifies not only changes in primary visual cortex but also re-weighting of decision weights at higher levels of the visual system; such mechanisms can underlie both specificity and transfer (e.g., Dosher & Lu, 2009). The distinct loci and mechanisms underlying plasticity when training does or does not include spatial covert attention are unknown. Differences in learning resulting from training with or without spatial covert attention could result from some combination of perceptual enhancement in early visual areas and their interaction with higher level decision-making areas.

Importantly, our results are due to attention during training, not attentional deployment during testing sessions. Selective attention can improve performance in Landolt square gap discrimination (Carrasco et al., 2002; Golla, et al., 2004; Montagna et al., 2009; Yeshurun & Carrasco, 1999) and in Vernier discrimination (Yeshurun & Carrasco, 1999), but no such modulation occurred during the testing sessions, as only neutral cues, used to distribute attention, were used. Indeed, the benefit for the attention group is more noteworthy when considering that during the post-test session observers in the neutral group were tested in exactly the same conditions in which they trained, whereas for observers in the attention group the post-test was not identical to the training sessions. Because training procedures for both groups were identical other than the attentional manipulation, our findings are not due to other factors known to influence VPL transfer, such as sensory adaptation (Harris et

al., 2012), variability in task difficulty (Hung & Seitz, 2014), task precision (Jeter et al., 2009), length of training (Jeter et al., 2010), stimulus feature reliability (Yashar & Denison, 2017) and exposure to stimuli at untrained locations prior to training (T. Zhang et al., 2010). We interpret our findings to demonstrate that the selective allocation of exogenous attention during training facilitates fine perceptual discrimination across locations and features.

Our Experiment 1 results are inconsistent with earlier findings that Landolt C acuity does not improve with training (Westheimer, 2001). On the contrary, we found improvement at the trained location and at the untrained location, with both selective and distributed attention. The learning effect was similar irrespective of training and testing conditions. We speculate that this finding could be attributed to some aspects of the task design. For example, it has been found that the inclusion of a pre-test at an untrained location facilitates transfer of learning from the fovea to the periphery (T. Zhang et al., 2010). In our experiment, we pre-tested observers at the to-be-untrained locations, which was perhaps sufficient location experience for learning to map onto. However, we did the same in Experiment 2, but location transfer was only partial. A second possible explanation is related to the fact that, in contrast to previous acuity studies (e.g., Fahle et al., 1995; Xiao et al., 2008), two locations were trained in Experiment 1 instead of just one location. Consistent with this idea is our previous finding of partial location transfer in an orientation discrimination task when observers trained at two locations (Donovan et al., 2015); however, that was not the case in another study in which two locations were also trained (Donovan & Carrasco, 2018). A third possibility regards the fact that observers in Experiment 1 were trained with a constant stimuli procedure, entailing a mixture of stimulus intensity and difficulty levels. A previous study found that, when observers train under such conditions instead of only at around threshold level, location transfer is more likely to occur (Hung & Seitz, 2014).

In Experiment 2, we found partial location transfer in the neutral group. This result is inconsistent with previous reports of location specificity in Vernier tasks (Fahle et al., 1995; Xiao et al., 2008). As we trained without location uncertainty, it is likely that observers endogenously attended to the trained location and that this could have facilitated partial transfer; however, we note that in the studies reporting location specificity observers also trained at one location. Thus, we think it is unlikely that the partial transfer we found would be due to location uncertainty during training.

A possible criticism of the results from Experiment 2 is that the pre-test threshold at the trained location for the trained orientation was higher in the neutral group than in the attention group. Such a difference could have allowed more room for improvement in the neutral group for the trained location or feature. That is, had the starting points for both groups been equal, the neutral group could have improved similarly between the trained and untrained. We think this is not the case for two reasons: (1) the pre-test thresholds between the two groups were not significantly different ($P > 0.1$), and (2) we analyzed the data after removing the observer with the highest pre-test threshold in the neutral group and the lowest pre-test threshold in the attention group. We found the same pattern of results regarding differences in location and feature specificity between groups—that is, location and feature specificity for the neutral group and location and feature transfer for the attention group. Likewise, in the neutral group, to have a similar starting point for both trained and untrained orientations, we analyzed the data after removing two additional observers with the largest difference between the pre-test thresholds at trained and untrained locations. We found the same pattern of results: an interaction between training and orientation due to significant learning at the trained but not at the untrained orientation.

As mentioned in the Introduction, other training regimens such as double training or interleaving multiple tasks have enabled learning and induced location and feature transfer of perceptual improvements. However, their practical application is limited by the reliance on training of a secondary task, which lengthens training and requires additional time and effort. Our training procedure offers an elegant and efficient alternative in that it requires only training on one task, can produce generalized learning after a short training period, and utilizes attentional resources during training only and not to perform the task.

Exogenous attention is a reliable tool for improving visual perception across the visual field and stimulus features (for reviews, see Carrasco, 2011; Carrasco & Barbot, 2015), which may have crucial clinical and expertise-developing applications. Importantly, exogenous attention is automatic and thus requires no additional effort or conscious awareness of the cue in order to improve performance. Perceptual learning training already represents an important tool for improving function of individuals with visual deficits. The potential for exogenous attention to further enhance visual improvements and generalization, with no additional time or effort and with only subtle changes to existing training protocols, makes it a very promising tool for rehabilitation.

This study expands on previous investigations from our lab that have isolated the effects of various types of attention on VPL. Our previous studies have revealed that training with either endogenous (Donovan & Carrasco, 2018) or exogenous (Donovan et al., 2015) spatial attention facilitates location transfer of learning and that exogenous attention enables learning (Szpiro & Carrasco, 2015). Our present study reveals several

novel findings. Exogenous attention facilitates location transfer for visual acuity tasks, which had been reported to be highly specific, thus suggesting that location transfer is facilitated in a wide range of tasks with different degrees of specificity. Further, this study also reveals that exogenous attention facilitates feature transfer; moreover, it can do so simultaneously while training on only one task at one location with one stimulus feature value. This line of research has revealed attention to be a powerful tool to enable, improve, and generalize VPL, which has important translational potential.

Keywords: perceptual learning, covert attention, visual acuity, location specificity, location generalization, feature specificity, feature generalization

Acknowledgments

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