

The impact of training on the inner–outer asymmetry in crowding

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Inner–outer asymmetry, where the outer anchor induces stronger crowding than the inner anchor, is a hallmark property of visual crowding. It is unclear the contribution of inner–outer asymmetry to the pattern of crowding errors (biased predominantly toward the anchor identities) and the role of training on crowding errors. In a typical radial crowding display, 20 observers were asked to report the orientation of a target Gabor (7.5° eccentricity) anchored by either an inner or outer Gabor along the horizontal meridian. The results showed that outer anchor conditions induced stronger crowding, accompanied by assimilative errors to the outer anchor for similar target/ anchor elements. In contrast, the inner anchor condition exhibited weaker crowding, with no significant patterns of crowding errors. A population coding model showed that the anchor weights in the outer anchor condition were significantly higher than those in the inner anchor condition. Nine observers continued to train the outer anchor condition for four sessions. Training reduced inner–outer asymmetry and reduced anchor weights to the outer anchor. The learning effects were retained over 4 to 6 months. Individual differences in the appearance of crowding errors, the strength of inner–outer asymmetry, and the training effects were evident. Nevertheless, our findings indicate that different crowding mechanisms may be responsible for the asymmetric crowding effects induced by inner and outer anchors, with the outer anchors dominating the appearance more than the inner ones. Training reduces inner–outer asymmetry by reducing target/ anchor confusion, and learning is persistent over months, suggesting that perceptual learning has the potential to improve visual performance by promoting neural plasticity.

Introduction

Crowding is the inability of recognizing an object with the presence of adjacent objects (or anchors) in the normal periphery and central vision in disorders such as amblyopia (Levi & Klein, 1985). It is considered to be an essential bottleneck or breakdown of object recognition (Strasburger, Rentschler, & Juttner, 2011; Whitney & Levi, 2011). Recent studies have established several diagnostic characteristics to distinguish crowding from other effects, such as masking, lateral interaction, and surround suppression (Levi, 2008; Whitney & Levi, 2011). One of the hallmark characteristics is inner–outer asymmetry, which demonstrates that the outer anchor (farther away from the fovea relative to the target) produces stronger interference than the inner one (closer to the fovea) (Bouma, 1970; Bouma, 1973). This seems unreasonable, as the inner anchor should be more distinguishable because of the better acuity for objects closer to the fovea and thus should be a stronger anchor. The inner–outer asymmetry has been found in different types of stimuli and tasks, such as Gabor orientation discrimination, letter recognition, and face recognition (Banks, Bachrach, & Larson, 1977; Bex, Dakin, & Simmers, 2003; Bouma, 1973; Farzin, Rivera, & Whitney, 2009; Petrov, Popple, & McKee, 2007).

Crowding is often attributed to abnormal integration of signals over space (Levi, Klein, & Hariharan, 2002; Pelli, Palomares, & Majaj, 2004) or limited attention resolution (He, Wang, & Fang, 1996; Intriligator & Cavanagh, 2001) because of insufficient spatial resolution to discern the target and anchors in the

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periphery. In terms of inner–outer asymmetry, several theories have been provided to account for it. The early account is associated with the cortical magnification factor (Pelli, 2008). It has been observed that, although the angular separations for inner and outer flankers are the same in visual space, the outer flanker is closer to the target than the inner one after mapping to cortical space; therefore, the outer flanker has more interference with the target (Motter & Simoni, 2007). Others have argued that the inner–outer asymmetry can be ascribed to the fact that increased receptive field sizes in the periphery bias the sampling rate toward the outer flanker (Dayan & Solomon, 2010) or leads to sparse selection in the visual periphery (Chaney, Fischer, & Whitney, 2014). Alternatively, inner–outer asymmetry can be explained in terms of attention allocation, which suggests that the asymmetrical deployment of attention outward leads to the selection of an outer flanker (Petrov & Meleshkevich, 2011a; Petrov & Meleshkevich, 2011b).

The measurements of errors observers made when reporting the identity of crowded targets provide an effective way to understand the mechanisms of crowding. Various models have been proposed to explain the systematic shift in the identity of crowded targets and the different types of errors: either reporting flanker identity (substitution errors) or reporting intermediate identities between the target and flankers (assimilation errors). Substitution models postulate that observers often misreport a flanker, causing substitution errors (Ester, Klee, & Awh, 2014; Ester, Zilber, & Serences, 2015). This substitution is attributed to the increased location uncertainty in the periphery (Krumhansl, 1977; Wolford, 1975; Zhang, Zhang, Liu, & Yu, 2012) or unfocused spatial attention (Strasburger, 2005; Strasburger, Harvey, & Rentschler, 1991), rendering the observers' failure to spatially differentiate between the target and the flankers. On the other hand, pooling or averaging models postulate that observers simultaneously detect and pool excessive information of low-level features, including those that belong to the flankers under crowding, as a result of inappropriate integration field size in the periphery (Freeman & Simoncelli, 2011; Greenwood, Bex, & Dakin, 2009; Harrison & Bex, 2015; Harrison, Mattingley, & Remington 2012; Keshvari & Rosenholtz, 2016; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). Population pooling models, which sum up responses for target and flanker features with different weights, were proposed to explain the perceptual effects of crowding, not only in features such as orientation, color, and spatial frequency (Greenwood, Bex, & Dakin, 2012; Greenwood & Parsons, 2020; Harrison & Bex, 2015; Pöder & Wagemans, 2007; van den Berg, Roerdink, & Cornelissen, 2010) but also in objects such as letters (Freeman, Chakravarthi, & Pelli, 2012) and faces (Kalpadakis-Smith, Gouaux, & Greenwood,

2018). For example, Harrison and Bex (2015) used a population pooling model that takes a weighted combination of population responses to the target and flankers to account for both substitution and averaging errors. Recently, Shechter and Yashar (2021) compared various mixture models and demonstrated that crowding reflects sampling over a weighted sum of the represented features, as the outer flanker was more heavily weighted compared to the inner one. These findings are in accord with recent models that account for crowding as population coding with weighted summation within receptive fields (Dayan & Solomon, 2010).

Researchers have been seeking effective ways to relieve crowding. Several studies have demonstrated that cueing of a crowded target location reduces the crowding effects (Anton-Erxleben & Carrasco, 2013; Kewan-Khalayly, Migó, & Yashar, 2022; Kewan-Khalayly & Yashar, 2022; Talgar, Pelli, & Carrasco, 2004; Yeshurun & Carrasco, 1999), and modulating attentional allocation could affect inner–outer asymmetry (Chakravarthi, Rubruck, Kipling, & Clarke, 2021; Kewan-Khalayly & Yashar, 2022; Kewan & Yashar, 2021; Petrov & Meleshkevich, 2011b). However, the role of attentional modulation has still been controversial, as some studies have reported that it has little or even no effect on crowding (Huckauf & Heller, 2002; Nazir, 1992; Scolaro, Kohlen, Barton, & Awh, 2007; Wilkinson, Wilson, & Ellemberg, 1997). In contrast, recent studies have demonstrated that crowding can be reduced by perceptual learning in typical and clinical populations (Chung, 2007; Chung, Li, & Levi, 2012; Huckauf & Nazir, 2007; Hussain, Webb, Astle, & McGraw, 2012; Malania, Pawellek, Plank, & Greenlee, 2020; Maniglia, Pavan, Cuturi, Campana, Sato, & Casco, 2011; Sun, Chung, & Tjan, 2010; Xiong, Yu, & Zhang, 2015; Yashar, Chen, & Carrasco, 2015; Zhu, Fan, & Fang, 2016). For example, Chung (2007) trained observers to identify the middle flanked letters in trigrams and showed that training strongly reduced the extent of crowding. Recently, we trained observers with a partial report task, in which the observers reported the central target letter of a three-letter string presented in the visual periphery, or a whole report task, in which the observers reported all three letters in order. We found that training indeed reduced crowding but did not reduce target misplacement errors or flanker substitution errors when these errors are normalized by the corresponding recognition errors. This disassociation between target recognition and flanker substitution errors supports the view that flanker substitution may be more likely a byproduct due to response bias rather than a cause of crowding (Xiong et al., 2015).

Although previous studies have demonstrated a training-induced reduction of crowding, it is still unknown whether inner–outer asymmetry could be

reduced by training, whether the learning transfers to untrained conditions, for how long the learning persists, and what mechanisms underlie this learning. In the present study, we first investigated the contribution of inner and outer flankers to the pattern of crowding errors in a radial Gabor orientation crowding display with an orientation identification task (Experiment 1). Then we introduced perceptual training paradigms to evaluate their effects on crowding (Experiment 2). Moreover, we investigated whether the benefit would still be there 4 to 6 months after training. We hope our results provide a more detailed understanding of the mechanism of the inner–outer asymmetry in crowding.

Methods

Observers and apparatus

A total of 20 observers (mean \pm age = 23.5 ± 4.4 years) with normal or corrected-to-normal vision participated in this study. Observers CYR, ZYW, and ZJY were coauthors and were experienced in psychophysical experiments. The others were new to psychophysical observations and were unaware of the purposes of the study. Written informed consent was obtained from all observers before data collection. This study was approved by the Peking University Institution Review Board.

The stimuli were generated with Psychtoolbox-3 (Pelli, 1997) and MATLAB (MathWorks, Natick, MA) and presented on a 21-inch G520 color monitor (Sony Corporation, Tokyo, Japan) with a resolution of 2048×1536 pixels and a 75-Hz refresh rate. The monitor was calibrated to give a mean luminance of 50 cd/m^2 . Observers viewed stimuli binocularly from a distance of 80 cm, with head movements minimized using a head and chin rest. Responses were given via a keypad. An EyeLink 1000 eye tracker (SR Research, Kanata, Ontario, Canada) was used to monitor eye movements. Trials with eye position deviations beyond 2° relative to the fixation dot were aborted and replaced by a new randomly generated trial.

Stimuli and procedures

In all experiments, the stimuli were a Gabor patch, a sinusoidal grating vignette by a Gaussian envelope with a spatial frequency of 5 cycles/degree and fixed contrast at 47%, in which ~ 1.5 periods of the sinusoidal pattern were visible. The center-to-center separation of the target and flankers was 2.25° . Observers were required

to maintain fixation on a circle with a 0.3° diameter and report the target orientation (clockwise [CW] or counterclockwise [CCW] from the vertical orientation). The target was presented at 7.5° eccentricity on the horizontal meridian of either left or right visual field (Figure 1A). The location of the visual field was randomly selected for each observer and was fixed across the test. Stimuli were presented for 425 ms after fixation (400 ms) and the next trial started 400 ms later than the response.

All 20 observers participated in Experiment 1 (Test 1) (Figure 1B). In Experiment 1, the target had nine orientations ($0^\circ, \pm 3^\circ, \pm 6^\circ, \pm 9^\circ, \pm 12^\circ$) and the flanker had six orientations ($0^\circ, \pm 30^\circ, \pm 60^\circ, -90^\circ$). There were three conditions: one unflanked condition (target without flanker) and two flanked conditions (target with an inner flanker or an outer flanker) (Figure 1A). In the unflanked condition, each block had six repeat trials per target orientation, giving 54 trials per block. In the flanked conditions, the target was presented either with an inner flanker or with an outer flanker in a separate block. Each block had two repeat trials per combination of orientation between target and flanker stimuli, giving 108 trials per block. Unflanked blocks were repeated four times, and flanked blocks were repeated 12 times each for inner and outer flankers. All 28 blocks were run following a permuted table to give a total of 2808 trials per observer, completed in two sessions. Each session consisted of 14 blocks and lasted for 1 hour. No feedback was provided. Before collecting the data, all observers were trained with each condition for one block to make sure they fully understood the test. In the experimental blocks, detailed instructions were displayed on the screen to remind the observers which stimulus to report on. The observer initiated the experiment with a key press when they understood the current task.

Because of time constraints, only nine observers from Experiment 1 were able to participate in Experiment 2 within 2 weeks. These observers continued to perform a training task for four sessions (Figure 1B). The training task was the flanked condition with an outer flanker as in Test 1. The target had nine orientations ($0^\circ, \pm 3^\circ, \pm 6^\circ, \pm 9^\circ, \pm 12^\circ$) and the outer flanker stimuli had six orientations ($0^\circ, \pm 30^\circ, \pm 60^\circ, -90^\circ$). Each block had two repeat trials per combination of orientation between target and flanker stimuli, giving 108 trials per block. Each training session consisted of 10 blocks (1080 trials in total) and no feedback was provided. The observers were tested again (Test 2) after four sessions of training to evaluate the training effects. Test 2 was the same as Test 1. To evaluate the retention effects, six observers of Experiment 2 were called back after 4 to 6 months (mean \pm age = 4.8 ± 0.4 months) to participate in a retention test. The retention test was the same as Test 1/Test 2.

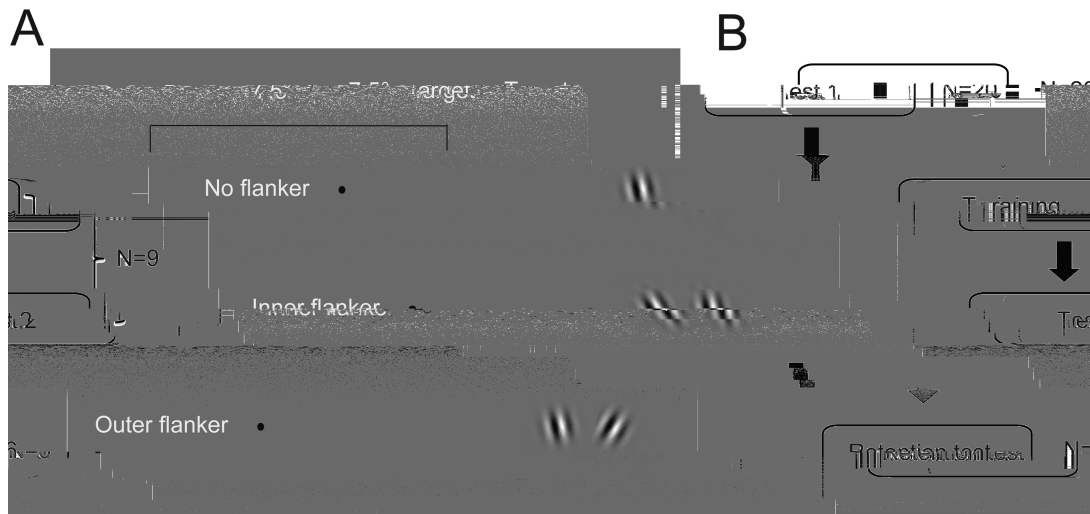


Figure 1. Stimuli and experimental design. (A) An example of stimuli. Observers were required to maintain fixation dot and report the orientation of the Gabor target (7.5° eccentricity) that was present alone or flanked by an inner or outer Gabor along the horizontal meridian. (B) Study design: All 20 observers participated in Test 1, and nine observers continued to perform a training task for four sessions; they were tested again (Test 2) after training. Six observers were called back and participated in a retention test after 4 to 6 months.

Analyses

In Experiments 1 and 2, psychometric functions were fit to data as a cumulative Gaussian function with three free parameters: midpoint or point of subjective equality (PSE) at 50%, slope, and lapse rate. Functions were fit separately for each observer and each flanker condition. Shifts in the midpoint were taken as changes in appearance (i.e., assimilation vs. repulsion errors). Thresholds were taken as the difference in the orientation required to shift performance from the midpoint to 75% CW responses, with a crowding index (or threshold elevation) obtained by dividing flanked thresholds by unflanked thresholds. The Greenhouse–Geisser correction was used when Mauchly’s test of sphericity had been violated (Greenhouse & Geisser, 1959).

Models

Data in Experiments 1 and 2 were fitted with a population coding model, which was similar to the prior models (Greenwood et al., 2012). This approach regarded crowding as the weighted combination of population responses to the target and flanker stimuli, which have previously been found to reproduce the systematic error that arise (Harrison & Bex, 2015). To simulate the crowding of orientation, a population coding model with four free parameters was conducted.

We first calculated the probabilistic effects of crowding to determine its strength of crowding. The

probabilistic effect of orientation crowding (ρ_θ) is defined as

$$\rho_\theta = \alpha \frac{-(\delta_\theta - \mu)^2}{2\sigma}$$

where δ_θ represents the orientation difference between target and flanker stimuli, σ sets the width of the tuning function (the first free parameter), α sets the peak of the tuning function (the second free parameter), and μ was centered on 0°.

If crowding occurs, the perceived target orientation (θ_c) with a weighted average of the orientation of target and flanker stimuli is defined as

$$\theta_c = w_t \theta_t + w_f \theta_f$$

where θ_t and θ_f are the veridical orientation of target and flanker stimuli, w_t is the weight of the target value in the average (the third free parameter), and w_f is the flanker weight (equal to $1 - w_t$).

The probability of a CW response (ρ_w) for each combined of target and flanker orientation is calculated as

$$\rho_w = \frac{1}{\sigma \sqrt{2\pi}} \int_{-\infty}^{\theta_c} \frac{-(\theta - \mu)^2}{2\sigma}$$

Results

Experiment 1: Dissociate distinct crowded errors in inner–outer asymmetry

In Experiment 1, 20 observers were asked to report the orientation of a target Gabor (CW or CCW from the vertical orientation) presented either isolated or with an inner flanker or an outer flanker. For each observer, psychometric functions were fit separately

for each condition to estimate the PSE (the 50% midpoint) and the thresholds (the difference from 50% to 75% CW responses). Example data are shown in Figures 2A to 2C. When unflanked, the judgments of target orientation (Figure 2C, black curve) transitioned rapidly from predominantly CCW to CW when the target orientation was around 0°. The psychometric function shows low bias in the PSE, with the steep slope indicating a low threshold. Psychometric functions of target performance with different flanker orientations were presented for the outer flanker condition and inner

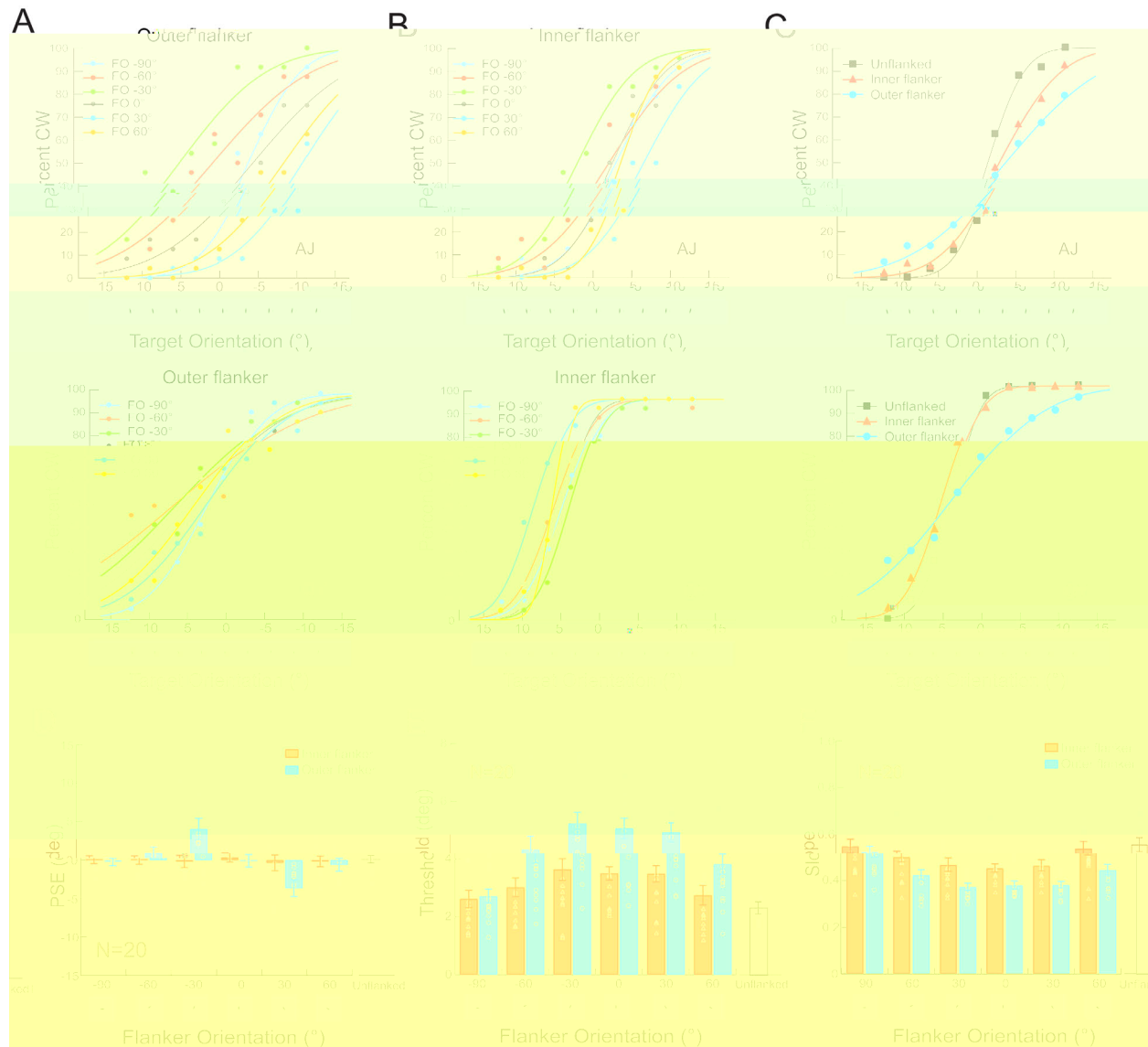


Figure 2. The crowding effect of target orientation identification (Experiment 1). (A–C) Psychometric functions with the proportion of CW responses plotted as a function of target orientation for two example observers (top, observer AJ; bottom, observer QY). Data are shown for a target with an outer flanker (A) or an inner flanker (B) for different flanker orientations. (C) The performance of target orientation identification with six flanker orientations was averaged. Data are shown for an unflanked target (black curve), a target with an inner flanker (red curve), and a target with an outer flanker (blue curve). (D–F) The PSE values, thresholds, and slopes for the unflanked (black bar), the inner flanker (red bar), and the outer flanker (blue bar) conditions were averaged over all observers across different flanker orientations. The gray symbols represent data for each observer. Error bars indicate 1 SEM.

anker condition (Figures 2A and 2B). In the outer anker condition (Figure 2A), the target judgments with a -90° anker (dark blue point) transitioned more rapidly and showed low bias in the PSE with a steep slope. In contrast, a -30° anker (light green) induced a strong bias toward a CW response, causing a leftward shift of the psychometric function in addition to the shallower slope. The opposite bias arose with a 30° anker (light blue). The data with the inner anker (Figure 2B) show the same pattern but with a weaker bias. To evaluate the general crowding effect, the performance of target orientation identification with six anker orientations ($0^\circ, \pm 30^\circ, \pm 60^\circ, -90^\circ$) was averaged. The results indicate that the outer anker (Figure 2C, blue circles and curve) induced stronger impairments in target performance than the inner anker did (Figure 2C, red triangles and curve), as shallower psychometric functions were observed in the outer anker condition. To see the bias in the PSE more specifically, the mean and individual PSE values were plotted as a function of anker orientation for anker conditions, and the mean and individual PSE values of the un-anker condition are provided in Figure 2D.

The mean thresholds of three conditions (un-anker, inner anker, and outer anker) are plotted as a function of anker orientation in Figure 2E. The mean threshold of the un-anker condition ($2.29^\circ \pm 0.93^\circ$) was plotted as a black bar. The thresholds of anker conditions were entered into a two-way analysis of variance (ANOVA) with anker condition (inner anker vs. outer anker) and anker orientation ($0^\circ, \pm 30^\circ, \pm 60^\circ, -90^\circ$) as the repeated measures. A significant difference in threshold between two different anker conditions was found, $(1, 19) = 28.12, p < 0.01, \eta^2 = 0.60$, with a lower threshold with the inner anker ($3.50^\circ \pm 1.25^\circ$) than with the outer anker ($4.82^\circ \pm 1.57^\circ$). A significant interaction effect between anker condition and anker orientation was also found, $(5, 95) = 4.80, p < 0.01, \eta^2 = 0.20$. Pairwise comparisons indicated that this interaction was mainly due to the significant difference in different anker orientations between inner and outer anker conditions ($p < 0.05$ for $0^\circ, \pm 30^\circ, \pm 60^\circ$).

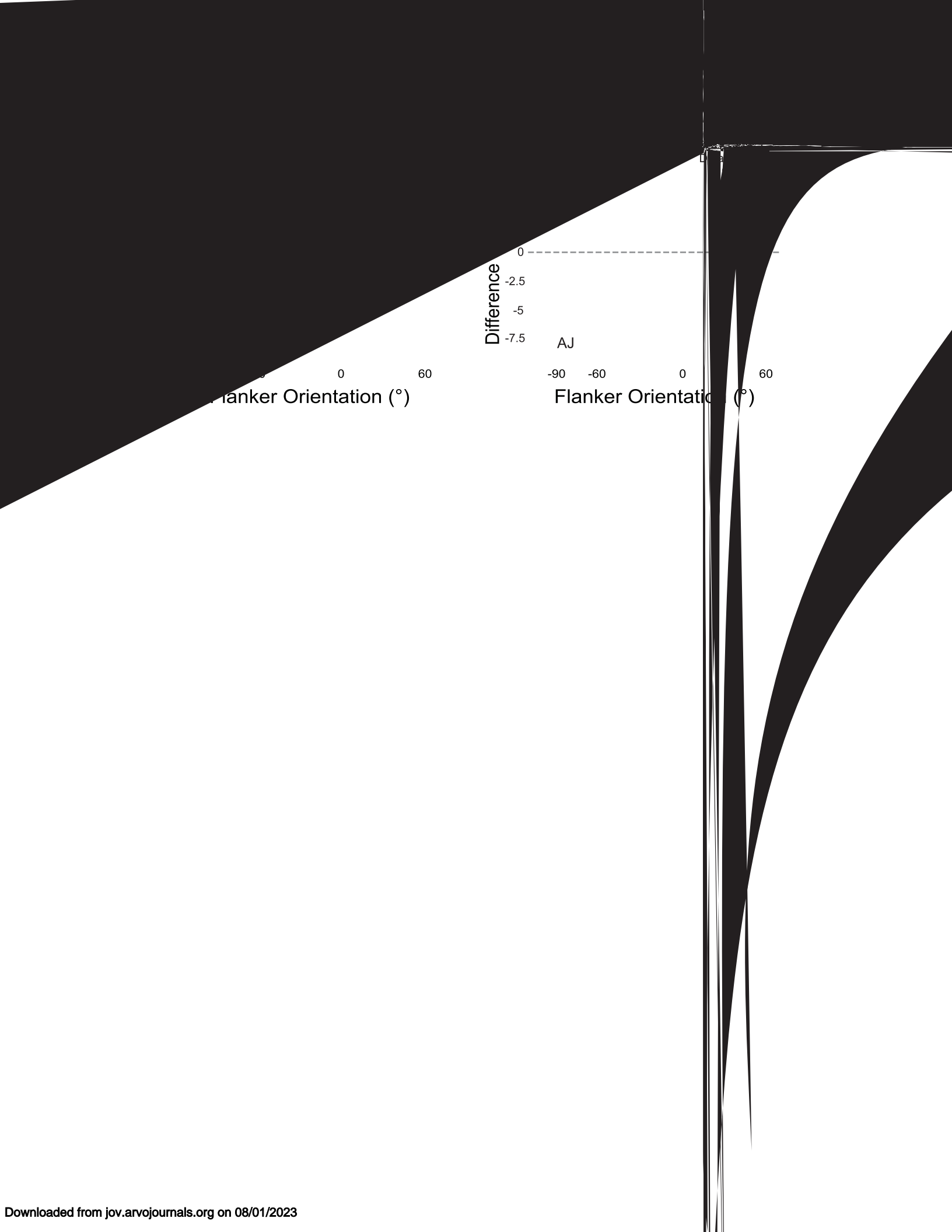
The slopes of the psychometric functions for anker conditions were also entered into a two-way ANOVA with anker condition (inner anker vs. outer anker) and anker orientation ($0^\circ, \pm 30^\circ, \pm 60^\circ, -90^\circ$) as the repeated measures. A significant difference in slope between two different anker conditions was found, $(1, 19) = 27.35, p < 0.01, \eta^2 = 0.59$, with a steeper slope with the inner anker (0.45 ± 0.10) than with the outer anker (0.38 ± 0.09) (Figure 2F).

To quantify the strength of the inner–outer asymmetry, we calculated the ratio of the threshold with the outer anker to that with the inner anker and adopted the criteria for inner–outer asymmetry from a recent study (Chakravarthi et al., 2021). Our results

showed that the ratio was significantly greater than 1 (mean = 1.46; $SD = 0.56$; $M = 3.61$; $N = 19$; $p < 0.01$, one-sample t -test), indicating a significant inner–outer asymmetry.

The mean difference of PSE values (the difference between ankered and un-anker conditions) are plotted as a function of anker orientation in Figure 3A. Two example datasets are shown in Figures 3B and 3C. A population coding model was used to fit these results (curves in Figures 3A to 3C). The PSE difference was then entered into a two-way ANOVA with anker condition (inner anker vs. outer anker) and anker orientation ($0^\circ, \pm 30^\circ, \pm 60^\circ, -90^\circ$) as the repeated measures. A significant main effect of anker orientation was found, $(5, 95) = 4.88, p < 0.01, \eta^2 = 0.20$. We also found a significant interaction effect of anker condition and anker orientation, $(1.63, 30.88) = 14.07, p < 0.01, \eta^2 = 0.43$, in the PSE difference. When the anker was presented outer (Figure 3A, blue circles), the PSE difference changed significantly with the -30° anker and 30° anker (all $p < 0.05$), indicating systematic crowded errors (assimilative errors, biased predominantly toward the anker identities). When the anker was presented inner (Figure 3A, red triangles), little changes in PSE difference were found (all $p > 0.05$). Examining these findings more closely, we can see that the observers showed two different systematic crowding errors. Some of them showed the assimilative errors (Figure 3B, red triangles), such that anker orientation moving toward CCW induced a positive PSE difference, indicating an increase in CCW response. In contrast, some others showed repulsive errors (Figure 3C, red triangles), such that anker orientation moving toward CCW induced a negative PSE difference. We conducted a paired-sample t -test to examine the difference of β , which represents the weights of the anker value of the inner anker or the outer anker. The results showed that the anker weights in the outer anker condition were significantly higher than those in the inner anker condition (Figure 3D), $t = -4.08, N = 19, p < 0.01$, suggesting that the observers tended to rely more on the anker orientation when identifying target orientation with an outer anker.

We found individual differences in the strength of inner–outer asymmetry, as not all observers showed high asymmetry (three out of 20 observers showed no inner–outer asymmetry) and crowding errors. Because Test 1 was completed in two separate sessions, we were able to compare the threshold, crowding index, slopes of the psychometric functions, and PSE difference between the first session and the second session of Test 1. These comparisons provide information about the reliability of observers' responses. Three-way ANOVA was conducted with anker condition (inner anker vs. outer anker), anker orientation ($0^\circ, \pm 30^\circ, \pm 60^\circ, -90^\circ$), and test time (first session vs. second session) as



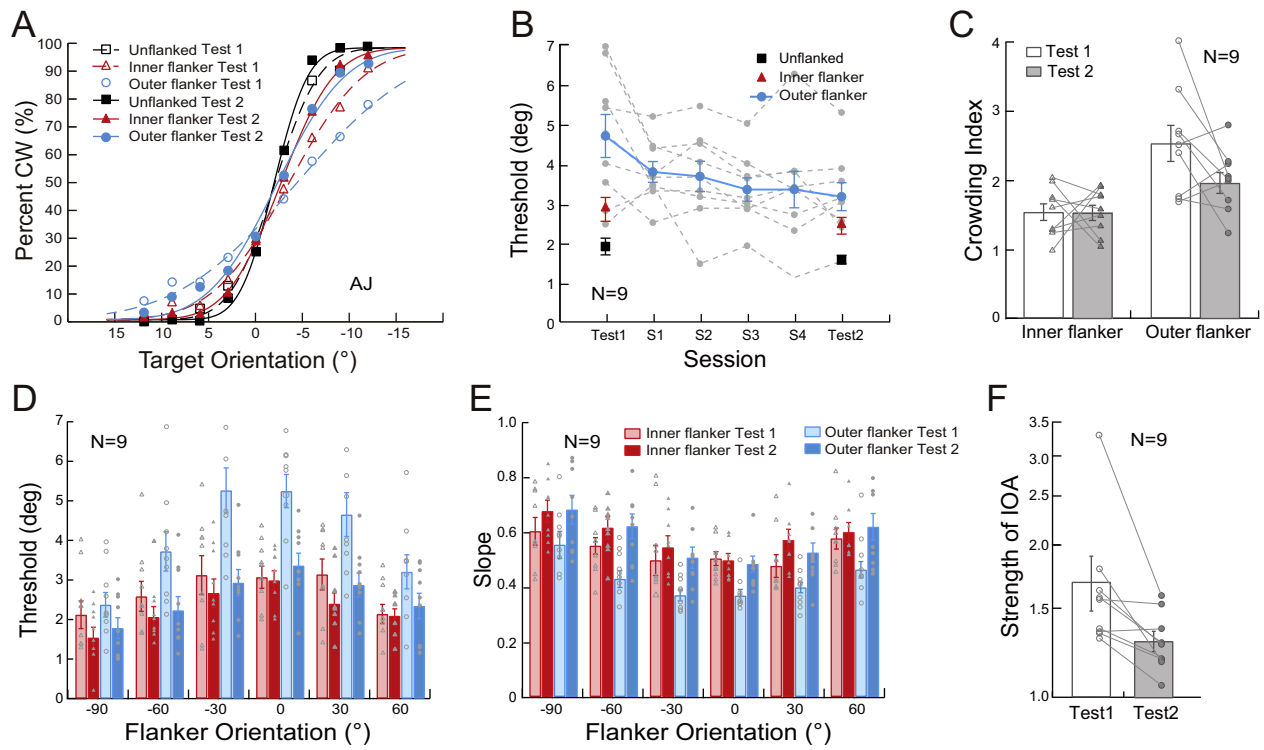


Figure 4. The effect of perceptual learning on inner–outer asymmetry (Experiment 2). (A) Psychometric functions for example data with the proportion of CW responses plotted as a function of target orientation. Data are shown for the unflanked condition (black squares), inner flanker condition (red triangles, untrained condition), and outer flanker condition (blue circles, trained condition) for Test 1 (dashed lines) and Test 2 (solid lines). (B) The mean and individual learning curve of thresholds through all sessions. The gray symbols indicate individuals’ data. (C) The crowding index of the unflanked conditions averaged over all observers for Test 1 and Test 2. The gray symbols indicate individuals’ data. (D, E) The threshold and slope for the unflanked condition averaged over all observers across different flanker orientations for Test 1 and Test 2. The gray triangles and circles represent data for each observer for a target with an

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difference (Figure 6C). Pairwise comparisons indicated that the threshold, slope, and crowding index showed significant changes between Test 1 and the retention test for the outer-anker condition (all $p < 0.05$). We also conducted a two-way ANOVA with anker condition (inner-anker vs. outer-anker) and test time (Test 1 vs. retention test) as the repeated measures to examine the change of β . We found a significant main effect of anker condition, $F(1, 5) = 6.97$, $p < 0.05$, $\eta^2 = 0.58$, and test time, $F(1, 5) = 7.13$, $p < 0.05$, $\eta^2 = 0.59$. A significant interaction effect among anker condition and test time was also found, $F(1, 5) = 8.49$, $p < 0.05$, $\eta^2 = 0.63$. Pairwise comparisons indicated a significant reduction in the weight of anker values in the outer-anked condition between Test 1 and the retention test ($p < 0.05$) (Figure 6D). These results indicate that the reduction of crowding through training is persistent for 4 to 6 months.

Discussion

By investigating different systematic errors of inner–outer asymmetry in crowding, we showed that outer-anker conditions induced a strong crowding effect, accompanied by stronger assimilative errors for the outer-anker for similar target/anker elements. In contrast, the inner-anker condition exhibited weak crowding, and no similar patterns of crowding errors were shown. A population coding model showed that the anker weights in the outer-anker condition were significantly higher than that in the inner-anker condition. Moreover, we found that four sessions of training reduced inner–outer asymmetry and reduced anker weights to the outer-anker. The learning effects were retained over 4 to 6 months. However, we also found individual differences in the appearance of crowding errors, the strength of inner–outer asymmetry, and the learning effects.

We replicated inner–outer asymmetry in the identification of Gabor patch orientation (Petrov & Meleshkevich, 2011a; Petrov & Meleshkevich, 2011b; Petrov et al., 2007; Shechter & Yashar, 2021). Our results are consistent with previous studies that demonstrated systematic errors biased by the appearance of the anker element in the perceived orientation of a crowded target (Ester et al., 2014; Greenwood et al., 2009; Harrison & Bex, 2015), and the outer-ankers dominate appearance more than the inner ones under crowding (Shechter & crow10.9589 0 0 10.(39 86.24(0.9586 0 10.9589 86.24179 539-281Us)33.3(o)2m [(coo)27(let(t)0.3(

for crowding. It has been argued that inner–outer asymmetry arises due to feature pooling where the weighted summation of available features is taken within receptive fields (Dayan & Solomon, 2010; Shechter & Yashar, 2021). It is speculated that training reduces

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