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The Critical Role of V2 Population Receptive Fields in Visual Orientation Crowding

Highlights

- Crowding effect correlates with the pRF size in V2
- Crowding effect modulates the pRF size in V2
- Perceptual training alleviates crowding and reduces the pRF size in V2

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In Brief

He et al. reveal that the pRF size of V2 is closely associated with the orientation crowding effect and suggest the pRFs of V2 as a bottleneck in visual crowding.



The Critical Role of V2 Population Receptive Fields in Visual Orientation Crowding

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SUMMARY

Crowding, the identification difficulty for a target in the presence of nearby flankers, is an essential bottleneck for object recognition and visual awareness [1, 2]. As suggested by multitudes of behavioral studies, crowding occurs because the visual system lacks the necessary resolution (e.g., small receptive field or high resolution of spatial attention) to isolate the target from flankers and therefore integrates them mistakenly [3–12]. However, this idea has rarely

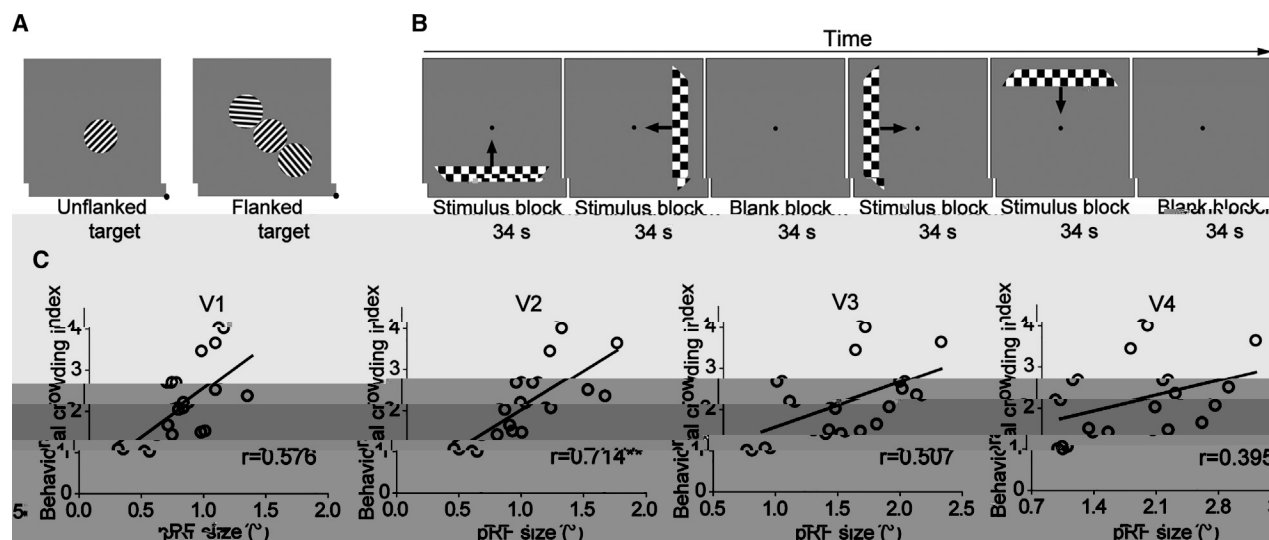


Figure 1. Stimuli, Procedure, and Results of Experiment 1

(A) Unflanked and flanked targets for measuring the magnitude of orientation crowding. The stimuli were presented in the upper left visual quadrant. (B) pRF mapping procedure. In a stimulus block, a horizontal or vertical checkered bar traversed through a circular aperture. Each run consisted of four stimulus blocks and two blank blocks. The two blank blocks always followed the second and the fourth stimulus block, respectively. (C) Correlations between the behavioral crowding index and the average pRF size of the target voxels in V1–V4 across individual subjects. Black dot represents the fixation point. Asterisks indicate a statistically significant correlation ($^{**}p < 0.01$).

checkered bar traversed through the visual field (Figure 1B). In other words, the mapping stimulus (i.e., the bar) was irrelevant to the crowding effect. We found that the pRF size of the target voxels increased systematically from V1 to V4 (mean \pm SEM; V1, $0.812^\circ \pm 0.058^\circ$; V2, $1.034^\circ \pm 0.086^\circ$; V3, $1.540^\circ \pm 0.108^\circ$; V4, $1.875^\circ \pm 0.173^\circ$), which is consistent with previous findings [13]. Then we calculated the correlation coefficients between the behavioral crowding index and the average pRF size of the target voxels in each visual area across individual subjects. We found that the correlation was significant in V2 ($r(14) = 0.714$; $p = 0.008$), but not in V1 ($r(14) = 0.576$; $p = 0.078$), V3 ($r(14) = 0.507$; $p = 0.168$), or V4 ($r(14) = 0.395$; $p = 0.427$; Figure 1C). Moreover, the correlation coefficient in V2 was significantly larger than those in V3 ($p = 0.035$) and V4 ($p = 0.005$), but not than that in V1 ($p = 0.099$). These results suggest a close relationship between the magnitude of the orientation crowding effect and the pRF size of the target voxels in V2.

Experiment 2: Attention-Dependent Modulation of the pRF Size in V2 by Crowding Effect

In experiment 1, because the pRF size in V2 and the crowding effect were measured independently and separately, the pRF size variation across subjects might not be ascribed to the crowding effect per se. In experiment 2, we manipulated the magnitude of the orientation crowding effect within subjects and examined whether the crowding magnitude could modulate the average pRF size of the target voxels in V2 and other visual areas. This experiment had two stimulus conditions—the parallel condition and the perpendicular condition, in which the orientation of the flankers was either parallel or perpendicular to that of the target (Figure 2A). Presumably, the parallel condition could elicit a stronger crowding effect than the perpendicular condition because of the similarity of the target and the flankers.

To facilitate the comparison between the psychophysical and fMRI results, the psychophysical part and the fMRI part of experiment 2 were designed similarly. In both parts, instead of presenting the crowding stimuli at a fixed location (as in experiment 1), the target and flankers rotated around the fixation point in steps of 20° every 2 s. Figure 2A shows all the eighteen possible locations where the stimuli were presented. In a 2-s trial, the target and flankers were always presented at one of the eighteen locations and subjects needed to discriminate an 800-ms orientation change of the target (Figure 2B). The target and flankers rotated 20° at the end of each trial. In the psychophysical part, we used the method of constant stimuli to measure the orientation discrimination thresholds (75% correct) for the target in the two stimulus conditions. The threshold in the parallel condition (mean \pm SEM: $5.371^\circ \pm 0.669^\circ$) was significantly higher than that in the perpendicular condition (mean \pm SEM: $3.552^\circ \pm 0.432^\circ$; paired-samples t test; $t(10) = 5.865$; $p < 0.001$). This finding demonstrated that the crowding effect induced by the parallel flankers was stronger than that induced by the perpendicular flankers, confirming the effectiveness of our manipulation.

In the fMRI part, we measured the pRF sizes in V1–V4 when subjects performed the orientation discrimination task with the target of the two stimuli (the attended session) or a demanding fixation task (the unattended session). The orientation changes of the target were always the orientation discrimination thresholds measured in the psychophysical part, ensuring that subjects could perform equally well in the two stimulus conditions. The rotating target and flankers served as the pRF mapping stimulus, which was relevant to the crowding effect in the attended session. The target voxels in experiment 2, as well as in experiments 3 and 4, were defined by the stimulus in Figure 2C, which covered all the areas swept by the rotating target. For each visual

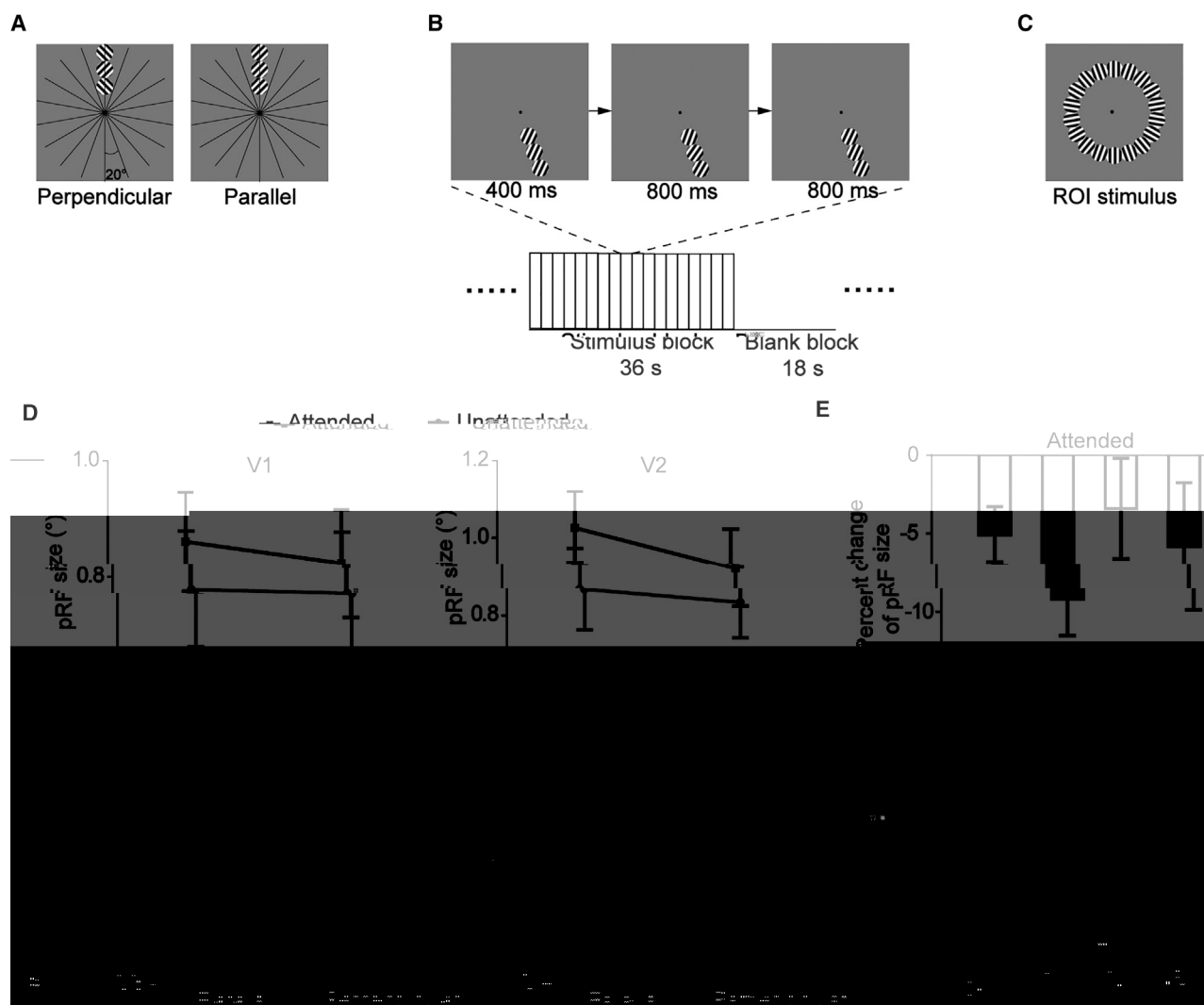


Figure 2. Stimuli, Procedure, and Results of Experiment 2

(A) Stimuli in the perpendicular and parallel conditions. The stimuli rotated around the fixation point in steps of 20° every 2 s. Radial lines (not shown during the experiment) indicate all the eighteen possible locations where the stimuli were presented.

(B) Procedure of experiment 2. Each stimulus condition had five runs of 270 s. Each run contained five stimulus blocks of 36 s, interleaved with five blank blocks of 18 s. A stimulus block consisted of eighteen discrimination trials of 2 s. In a discrimination trial, the target and flankers were always presented at one of the eighteen possible locations and the orientation of the target was changed by α° (α : 1, 3, 5, 7, and 9) between 400 and 1,200 ms after the onset of the trial, either clockwise or counterclockwise. Subjects needed to judge the direction of the orientation change. The target and flankers rotated 20° around the fixation point at the end of each trial.

(C) Region of interest (ROI) stimulus for localizing the target voxels.

(D) pRF sizes in V1–V4 for the two stimulus conditions and the two attention conditions.

(E) Percent changes of the pRF sizes in V1–V4 from the parallel condition to the perpendicular condition. The asterisk indicates that the percent change of the pRF size was significantly below zero ($p < 0.05$). Error bars denote 1 SEM calculated across subjects.

area, we performed a two-way repeated-measures ANOVA with stimulus configuration (parallel versus perpendicular) and attention (attended versus unattended) as within-subject factors (Figure 2D). We found that the main effect of stimulus configuration was significant in V2 ($F_{1,10} = 20.252$; $p < 0.001$), but not in V1 ($F_{1,10} = 1.992$; $p = 0.565$), V3 ($F_{1,10} = 0.182$; $p = 0.989$), or V4 ($F_{1,10} = 0.809$; $p = 0.862$). The main effect of attention was significant in V2 ($F_{1,10} = 29.071$; $p < 0.001$) and V3 ($F_{1,10} = 21.872$; $p = 0.004$), but not in V1 ($F_{1,10} = 3.054$; $p = 0.375$) or V4 ($F_{1,10} = 0.835$; $p = 0.854$). The interaction between stimulus configuration and

attention was significant in V2 ($F_{1,10} = 9.530$; $p = 0.047$), but not in V1 ($F_{1,10} = 1.308$; $p = 0.730$), V3 ($F_{1,10} = 1.971$; $p = 0.572$), or V4 ($F_{1,10} = 3.422$; $p = 0.326$). These results suggest that the orientation crowding might have different effects on the average pRF size of the target voxels in the attended and unattended conditions. Furthermore, we calculated the percent change of the pRF size across the two stimulus conditions as $(Size_{perpendicular} - Size_{parallel}) / Size_{parallel} \times 100\%$, where $Size_{perpendicular}$ and $Size_{parallel}$ are the average pRF sizes of the target voxels in the perpendicular and parallel conditions,

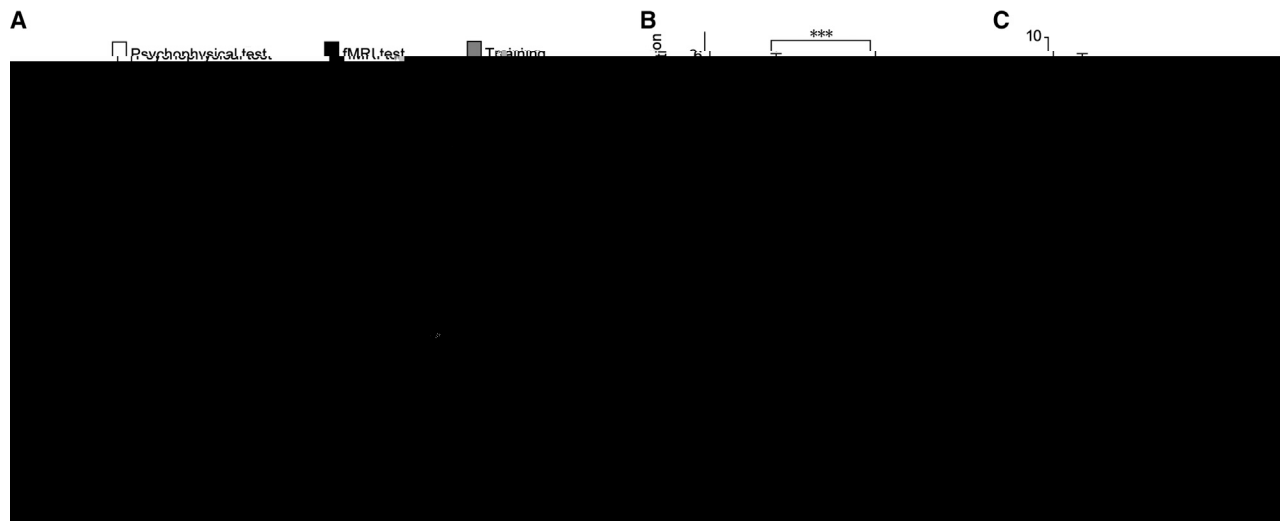


Figure 3. Protocol and Results of Experiment 3

(A) Protocol. Subjects underwent five daily training sessions. Psychophysical and fMRI tests were performed before and after training. (B) Orientation discrimination thresholds for the crowded target in the pre- and post-training tests. Asterisks indicate that subjects' orientation discrimination thresholds after training were significantly smaller than those before training ($***p < 0.001$). (C) Percent changes of the pRF sizes in V1–V4 from the pre-training test to the post-training test. Asterisks indicate that the percent change of the pRF size was significantly below zero ($***p < 0.001$). (D) Correlations between the percent improvement in orientation discrimination performance with the crowded target and the percent change of the pRF size in V1–V4. Asterisks indicate a significant correlation ($***p < 0.001$). Error bars denote 1 SEM calculated across subjects.

respectively (Figure 2E). In the attended session, when subjects performed the orientation discrimination task with the target, one-sample *t* tests revealed that the percent change was significantly less than zero in V2 ($t(10) = 3.866$; $p = 0.012$), but not in V1 ($t(10) = 2.849$; $p = 0.066$), V3 ($t(10) = 1.065$; $p = 0.776$), or V4 ($t(10) = 1.430$; $p = 0.554$). Moreover, paired-samples *t* tests revealed that the percent change in V2 was significantly larger than those in V1 ($t(10) = 2.248$; $p = 0.048$) and V3 ($t(10) = 2.585$; $p = 0.027$), but not in V4 ($t(10) = 1.418$; $p = 0.187$). Given that subjects' response accuracies during the pRF mapping were not significantly different between the two stimulus conditions (parallel, $75.211\% \pm 1.552\%$; perpendicular, $76.346\% \pm 1.291\%$; paired-samples *t* test; $t(10) = 0.678$; $p = 0.513$), the observed effect should not be attributed to differences in task performance and attentional state. In the unattended session, when subjects performed a fixation task, one-sample *t* tests revealed that the percent change was not significantly different from zero (V1, $t(10) = 0.163$, $p = 0.999$; V2, $t(10) = 1.275$, $p = 0.650$; V3, $t(10) = 1.259$, $p = 0.661$; V4, $t(10) = 0.599$, $p = 0.963$). These results demonstrated that the average pRF size of the target voxels in V2 was significantly smaller when the crowding effect was weak than when the crowding effect was strong. And this pRF size modulation was found only when subjects paid attention to the target.

Experiment 3: Learning to Reduce Crowding Shrinks the pRF in V2

We employed a perceptual learning paradigm [15–17] to reduce the crowding effect and examined whether and how reducing the crowding effect would change the average pRF size of the target voxels in V2 and other visual areas. Experiment 3 consisted of three phases: pre-training test, orientation discrimination

training with the flanked target, and post-training test (Figure 3A). For all the three phases, the visual stimulus (only the parallel stimulus was used), task, and procedures in the psychophysical and fMRI parts were similar to those in the attended session of experiment 2. Specifically, the target and flankers rotated around the fixation point and subjects performed the orientation discrimination task with the flanked target.

Consistent with previous findings [18], perceptual learning did reduce the crowding effect. After five daily training sessions, subjects' orientation discrimination thresholds with the flanked target in the post-training test were significantly smaller than those in the pre-training test (paired-samples *t* test; $t(10) = 6.140$; $p < 0.001$; Figure 3B). Their behavioral percent improvement was calculated as $(Threshold_{pre-training} - Threshold_{post-training}) / Threshold_{pre-training} \times 100\%$, where $Threshold_{pre-training}$ and $Threshold_{post-training}$ are the orientation discrimination thresholds in the pre- and post-training tests, respectively. The percent improvement was $43.690\% \pm 6.216\%$ (mean \pm SEM), which was significantly larger than zero (one-sample *t* test; $t(10) = 7.029$; $p < 0.001$).

In the fMRI part of the pre- and post-training tests, the rotating target and flankers served as the pRF mapping stimulus and we measured the pRF sizes in V1–V4 when subjects performed the orientation discrimination task with the target. The orientation changes of the target were always the orientation discrimination thresholds measured in the psychophysical part, ensuring that subjects could perform equally well in the two test phases. The percent change of the pRF size after training was calculated as $(Size_{post-training} - Size_{pre-training}) / Size_{pre-training} \times 100\%$, where $Size_{pre-training}$ and $Size_{post-training}$ are the average pRF sizes of the target voxels in the pre- and post-training tests, respectively. One-sample *t* tests revealed that the percent change of the pRF size after training was significantly less than zero in V2

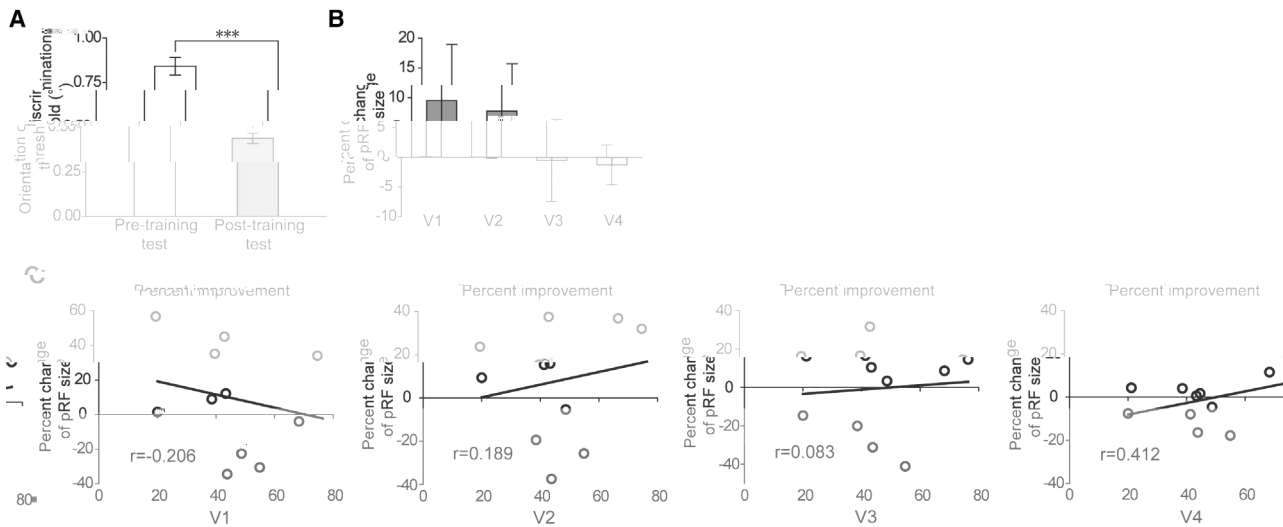


Figure 4. Results of Experiment 4

(A) Orientation discrimination thresholds for the unflanked target in the pre- and post-training tests. Asterisks indicate that subjects' orientation discrimination thresholds after training were significantly smaller than those before training (** $p < 0.001$).

(B) Percent changes of the pRF sizes in V1–V4 from the pre-training test to the post-training test.

(C) Correlations between the percent improvement in orientation discrimination performance with the unflanked target and the percent change of the pRF size in V1–V4. Error bars denote 1 SEM calculated across subjects.

($t(10) = 5.087$; $p < 0.001$), but not in V1 ($t(10) = 0.330$; $p = 0.996$), V3 ($t(10) = 1.570$; $p = 0.471$), or V4 ($t(10) = 0.856$; $p = 0.880$; Figure 3C). In other words, the average pRF size of the target voxels in V2 decreased significantly following the perceptual training. Given that subjects' response accuracies during the pRF mapping were not significantly different between the two test phases (pre-training, $73.727\% \pm 2.591\%$; post-training, $73.348\% \pm 2.622\%$; paired-samples t test; $t(10) = 0.153$; $p = 0.882$), the observed pRF size change in V2 should not be attributed to differences in task performance and attentional state.

Furthermore, we calculated the correlation coefficients between the behavioral percent improvement and the percent change of the pRF size in V1–V4 across individual subjects. The correlation was significant in V2 ($r(9) = -0.866$; $p < 0.001$), but not in V1 ($r(9) = -0.241$; $p = 0.924$), V3 ($r(9) = -0.483$; $p = 0.432$), or V4 ($r(9) = -0.188$; $p = 0.969$; Figure 3D). Moreover, the correlation coefficient in V2 was significantly larger than those in V1 ($p < 0.001$), V3 ($p < 0.001$), and V4 ($p < 0.001$). The more the reduction of the pRF size in V2, the stronger the learning effect to reduce the orientation crowding. These results provide causal evidence for the critical role of the V2 pRF size in visual crowding.

Experiment 4: Little pRF Size Change after Orientation Discrimination Training with the Unflanked Target

It might be argued that the pRF size reduction observed in experiment 3 was caused by some general perceptual learning effect, rather than the reduction of the crowding effect per se. To examine this issue, we performed experiment 4, which was very similar to experiment 3 except that subjects were trained and tested with the orientation discrimination task with the unflanked target.

After training, subjects' orientation discrimination thresholds decreased significantly (paired-samples t test; $t(10) = 6.489$;

$p < 0.001$; Figure 4A). The percent improvement of their behavioral performance was $45.560\% \pm 5.125\%$ (mean \pm SEM), which was significantly larger than zero (one-sample t test; $t(10) = 8.891$; $p < 0.001$) and was comparable to the behavioral learning effect in experiment 3. We failed to find any significant pRF size change in any of the four areas (one-sample t test; V1, $t(10) = 1.009$, $p = 0.807$; V2, $t(10) = 0.976$, $p = 0.824$; V3, $t(10) = 0.078$, $p = 0.999$; V4, $t(10) = 0.389$, $p = 0.992$; Figure 4B). Furthermore, there was no significant correlation between the behavioral percent improvement and the percent change of the pRF size in any of the four areas across individual subjects (V1, $r(9) = -0.206$, $p = 0.956$; V2, $r(9) = 0.189$, $p = 0.968$; V3, $r(9) = 0.083$, $p = 0.999$; V4, $r(9) = 0.412$, $p = 0.607$; Figure 4C). These results suggest that the pRF size reduction in V2 after training is associated with the reduction of the crowding effect rather than a general perceptual learning effect.

DISCUSSION

Using the non-invasive fMRI-based pRF technique in combination with psychophysics, our study has the following major findings. First, even when the magnitude of the orientation crowding effect and the average pRF size of the target voxels in V2 were measured independently, they were positively correlated across subjects. Second, the average pRF size of the target voxels in V2 in the strong crowding condition was larger than that in the weak crowding condition. Third, perceptual training improved subjects' orientation discrimination performance with the crowded target. Meanwhile, it reduced the average pRF size of the target voxels in V2. These two changes were remarkably correlated. Taken together, these findings provide consistent evidence that the orientation crowding effect is closely associated with the average pRF size of the target voxels in V2—the smaller

the pRF, the weaker the crowding effect. Meanwhile, it is noteworthy that V1 exhibited marginally significant effects in experiments 1 and 2, suggesting that V1 pRFs might also contribute to the orientation crowding.

Our study attempts to address the long-standing and central question in visual crowding—the “bottleneck” question. Crowding is usually attributed to inappropriate integration or pooling of

metamer. In their model, the first stage decomposes an image with a population of oriented V1-like receptive fields. The second stage computes averages of nonlinear combinations of these responses over regions that scale in size linearly with eccentricity, according to a scaling constant that can be varied parametrically. Given a photographic image, the authors synthesized distinct images with identical model responses and asked whether human observers could discriminate them. From these behavioral data, they estimated the scaling constant that yields metameric images and found that it was consistent with receptive field sizes in V2, suggesting a functional role of this area in information pooling in the periphery. Interestingly, this model can predict degradations of peripheral recognition (i.e., crowding) as a function of both spacing and eccentricity.

Although both the modeling work and our experimental data point to a key role of V2 in orientation crowding, the bottleneck of visual crowding could also exist in other brain areas and networks. This is because the current study only tested low-level orientation discrimination with the crowding stimuli. It has been confirmed that crowding occurs at multiple levels in the visual processing hierarchy [40–43]. For example, Louie et al. [41] demonstrated a holistic crowding between high-level face representations, suggesting that face-selective areas might play a role in this kind of crowding. It should also be noted that, together with previous fMRI studies [44, 45], the current study also suggests that spatial attention or attention resolution is a critical component in the bottleneck. The pRF size change manifested only when subjects' attention was allocated to the crowded targets. In the future, it is worthwhile to examine whether and how crowding is determined by the combination of bottlenecks at multiple levels of cortical processing, including intracortical interaction and high-level attention.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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AUTHOR CONTRIBUTIONS

D.H. and F.F. designed the experiments. D.H. collected the data. D.H. and F.F. analyzed the data. D.H., Y.W., and F.F. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

LEAD CONTACT AND MATERIALS AVAILABILITY

500 ms blank interval. Subjects were asked to maintain fixation on a central black dot throughout the experiment, and make a 2-alternative-forced-choice (2-AFC) judgment of the orientation of the second target relative to the first one (clockwise or counterclockwise). In a block, each of the five θ values was used eight times.

Before measuring pRFs in visual cortex, we defined retinotopic visual areas (V1, V2, V3, and V4) using a standard phase-encoded method developed by Sereno et al. [47] and Engel et al. [48] in which subjects viewed a rotating wedge and an expanding ring that created traveling waves of neural activity in visual cortex. We also performed a block-design run to identify the voxels in the retinotopic areas responding to the target. These voxels are termed target voxels in this study. The run contained twelve stimulus blocks of 12 s, interleaved with twelve blank blocks of 12 s. The stimulus was identical to the target, except that its orientation was randomly selected between 0° and 180° . It was presented at 5Hz in the stimulus blocks.

Voxel-wise pRF parameters were estimated using the method described in Dumoulin and Wandell [13]. Specifically, hemodynamic response function (HRF) was measured for each subject in a separate run. This run contained 12 trials. In each trial, a flickering full contrast checkered disk with a radius of 10° was presented for 2 s, followed by a 30 s blank interval. The HRF was estimated by fitting the convolution of a 6-parameter double-gamma function with a 2 s boxcar function to the BOLD response elicited by the disk.

Four pRF mapping runs were performed in which a flickering full contrast checkered bar (2° in width) traversed through a circular aperture with a radius of 10° around fixation (i.e., the mapped visual area) (Figure 1B). The bar moved through two orientations (vertical and horizontal) in two opposite directions, resulting in a total of four different stimulus configurations. Each run contained four stimulus blocks of 34 s, one for each stimulus configuration, and two blank blocks of 34 s. In a run, the order of the four stimulus configurations was randomized, but the two blank blocks always followed the second and the fourth stimulus blocks, respectively. In a stimulus block, the bar traversed through the mapped visual area in 17 steps of 1.125° within 34 s. Throughout these runs, subjects performed a color discrimination task at fixation to maintain fixation and control attention.

Experiment 2

This experiment had two stimulus conditions – the parallel condition and the perpendicular condition (Figure 2A). In both conditions, the target was centered at 6.25° eccentricity with two abutting flankers positioned radially. The target and flankers rotated around the fixation point. At the starting position as shown in Figure 2A, the orientation of the target was 45° , either left or right tilted. In the parallel condition, the flankers were parallel to the target. In the perpendicular condition, the flankers were perpendicular to the target. The former condition presumably elicited a stronger crowding effect than the latter condition.

In the psychophysical part of Experiment 2, we used the method of constant stimuli to measure orientation discrimination thresholds (75% correct) for the target in the parallel and perpendicular conditions. Each condition had five runs of 270 s. Each run contained five stimulus blocks of 36 s, interleaved with five blank blocks of 18 s (Figure 2B). A stimulus block consisted of eighteen discrimination trials of 2 s. In a discrimination trial, the target and flankers were always presented at one of the eighteen possible locations as shown in Figure 2A and the orientation of the target was changed by α° (α : 1, 3, 5, 7, 9) between 400 and 1200 ms after the onset of the trial, either clockwise or counterclockwise. Subjects were asked to maintain fixation and made a 2-AFC judgment of the direction of the orientation change. The target and flankers rotated 20° around the fixation point at the end of each trial. Only one of the five α values was used in a stimulus block.

In the fMRI part of Experiment 2, we estimated pRF parameters when subjects performed the orientation discrimination task in the two stimulus conditions. The stimuli were identical to those in the psychophysical part except that a rapid serial visual presentation (RSVP) of letters was added at fixation. The fMRI part had two sessions: the attended session and the unattended session. In the attended session, the procedure was similar to that of the psychophysical part, except that the orientation change of the target was always the measured discrimination threshold for each stimulus condition. There were three functional runs of 270 s in each stimulus condition. The unattended session was identical to the attended session, except that subjects performed a very demanding RSVP task at fixation in the stimulus blocks, rather than the orientation discrimination task with the target. In the RSVP task, subjects were asked to detect two targets (X and Y) in a stream of distractors (Z, L, N, and T). Each letter subtended 0.27° of visual angles and was presented for 0.2 s.

In Experiment 2, the same procedures as those in Experiment 1 were used to estimate the HRF and to define V1-V4 and target voxels. The only difference was that the stimulus used for defining target voxels consisted of eighteen gratings that had the same physical parameters as the target in the fMRI part (Figure 2C). The region occupied by the stimulus was exactly the area swept by the rotating target in this experiment.

Experiment 3

This perceptual learning experiment consisted of three phases (Figure 3A): pre-training test (days 1-2), orientation discrimination training (days 3-7), and post-training test (days 8-9). For all the three phases, the visual stimulus (only the parallel stimulus was used), task, and procedures in the psychophysical and fMRI parts were similar to those in the attended session of Experiment 2. The fMRI runs for estimating the HRF and defining V1-V4 and target voxels in Experiment 3 were the same as those in Experiment 2.

During the two test phases, we first measured the orientation discrimination thresholds (75% correct) with the target on days 1 and 8, respectively. The fMRI part was conducted on days 2 and 9 to estimate the pRF parameters of the target voxels, respectively. The measured thresholds on days 1 and 8 were used as the orientation change of the target (i.e., α°) in the fMRI part on days 2 and 9, respectively.

During the training phase, each subject underwent five daily training sessions outside the MRI scanner. Each daily session consisted of eighteen runs – thirteen training runs and five threshold estimation runs. The training runs were similar to those in the fMRI part, except that a high-pitched tone was provided after an incorrect response. In the training runs, the orientation change

of the target was the orientation discrimination threshold that was measured in the five threshold estimation runs on the immediately preceding day. The threshold estimation runs were identical to those in the psychophysical part of the two test phases.

Experiment 4

The procedure and design of Experiment 4 were similar to those of Experiment 3, except that the target were presented without flankers.

QUANTIFICATION AND STATISTICAL ANALYSIS

To estimate the orientation discrimination thresholds, for each condition and subject, data from all runs were pooled together for analysis. The percentage of trials in which subjects made a correct response was plotted as a psychometric function of θ or α . We used a cumulative normal function to fit the psychometric values and interpolated the data to find the 75% accuracy point (i.e., the orientation discrimination threshold).

MRI data were processed using BrainVoyager QX (Brain Innovations, Maastricht, the Netherlands) and custom scripts in MATLAB (Mathworks). The anatomical volume in the retinotopic mapping session was transformed into the Talairach space and then inflated using BrainVoyager QX. Functional volumes in all sessions were preprocessed, including 3D motion correction, linear trend removal, and high-pass filtering (cut-off frequency: 0.015 Hz) using BrainVoyager QX. No subject exhibited excessive head movement (< 2 mm in translation, $< 0.5^\circ$ in rotation) within any fMRI session. The functional volumes were then aligned to the anatomical volume in the retinotopic mapping session and transformed into the Talairach space. The first 6 s of BOLD signals were discarded to minimize transient magnetic saturation effects.

A general linear model (GLM) procedure was used to define target voxels. Target voxels in V1-V4 were defined as those voxels that responded more strongly to the stimulus than the blank screen ($p < 10^{-3}$, uncorrected) in the localizer run. We estimated pRF parameters for each target voxel using the method proposed by Dumoulin and Wandell [13]. The predicted BOLD signal was calculated from the known visual stimulus parameters, the HRF, and a model of the joint receptive field of the underlying neuronal population. This model consisted of a two-dimensional Gaussian pRF with parameters x_0 , y_0 , and σ , where x_0 and y_0 are the coordinates of the center of the receptive field, and σ indicates its spread (standard deviation) or size. All parameters were stimulus-referred, and their units were degrees of visual angle. These parameters were adjusted to obtain the best possible fit of the measured BOLD signal. Only the voxels whose pRF model could explain at least 15% of the variance of the raw data were included for further analyses. Given that the time course of BOLD signal consisted of 102 (Experiment 1) and 135 (Experiments 2, 3, and 4) TRs, this threshold corresponded to a significance level of $p < 0.001$ (uncorrected) [49]. In both the psychophysical and fMRI data analyses, Bonferroni correction was applied with statistical tests involving multiple comparisons.

DATA AND CODE AVAILABILITY

fMRI and behavioral data are available upon request by contacting the Lead Contact, Fang Fang (ffang@pku.edu.cn).