Two-stage perceptual learning to break visual crowding

Ziyun Zhu*
Department of Psychology and Beijing Key Laboratory of Behavior and Mental Health
Key Laboratory of Machine Perception (Ministry of Education)
Peking-Tsinghua Center for Life Sciences
PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing, P.R. China

Zhenzhi Fan*
Department of Psychology and Beijing Key Laboratory of Behavior and Mental Health
Key Laboratory of Machine Perception (Ministry of Education)
Peking-Tsinghua Center for Life Sciences
PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing, P.R. China

Fang Fang
Department of Psychology and Beijing Key Laboratory of Behavior and Mental Health
Key Laboratory of Machine Perception (Ministry of Education)
Peking-Tsinghua Center for Life Sciences
PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing, P.R. China

When a target is presented with nearby flankers in the peripheral visual field, it becomes harder to identify, which is referred to as *crowding*. Crowding sets a fundamental limit of object recognition in peripheral vision, preventing us from fully appreciating cluttered visual scenes. We trained adult human subjects on a crowded orientation discrimination task and investigated whether crowding could be completely eliminated by training. We discovered a two-stage learning process with this training task. In the early stage, when the target and flankers were separated beyond a certain distance, subjects acquired a relatively general ability to break crowding, as evidenced by the fact that the breaking of crowding could transfer to another crowded orientation, even a crowded motion stimulus, although the transfer to the opposite visual hemi-field was weak. In the late stage, like many classical perceptual learning effects, subjects' performance gradually improved and showed specificity to the trained orientation. We also found that, when the target and flankers were spaced too finely, training could only reduce, rather than completely eliminate, the crowding effect. This two-stage learning process illustrates a learning strategy for our brain to deal with the notoriously difficult problem of identifying peripheral objects in clutter. The brain first learned to solve the "easy and general" part of the problem (i.e., improving the processing resolution and segmenting the target and flankers) and then tackle the "difficult and specific" part (i.e., refining the representation of the target).

Introduction

In peripher l vision, one's bility to identify t rget is impeded by ne rby fl nkers. This phenomenon is known s *crowding* (Levi, 2008; Whitney & Levi, 2011). Crowding h s been reported to occur with m ny kinds of stimuli nd t sks, such s letter recognition (oum , 1 70), vernier cuity (Levi, Klein, & itseb omo, 1 85), orient tion discrimin tion (Westheimer, Shim - mur , & McKee, 1 76), stereo cuity (utler & Westheimer, 1 78), nd f ce recognition (Louie, ressler, & Whitney, 2007). It sets fund ment l limit on visu l perception nd conscious w reness in the periphery.

M ny theories h ve been dv nced to expl in visu l crowding (Levi, 2008). Most of the theories

Citation: Zhu, Z., Fan, Z., & Fang, F. (2016). Two-stage perceptual learning to break visual crowding. *Journal of Vision*, *16*(6):16, 1–12, doi:10.1167/16.6.16.

doi: 10.1167/16.6.16 Received August 14, 2015; published April 22, 2016. ISSN 1534-7362

posit th t t some st ge of peripher l inform tion processing, the visu l system l cks the necess ry resolution (constr ined by retin l/cortic l s mpling nd/or sp ti l ttention) to process the t rget individu lly when it is surrounded by ne rby fl nkers. ec use of the limited resolution, fe tures from the t rget nd fl nkers re mist kenly inte- gr ted, resulting in nonveridic l percept. owever, it is still highly controversi l where the resolution bottleneck is in the visu l processing stre m. The two most popul r theories for crowding h ve pl ced the bottleneck t the level of bottom-up fe ture pooling (Levi, rih r n, & Klein, 2002; Pelli & Tillm n, 2008) or ttention l selection (e, C v n gh, & Intrilig tor, 1 6; Intrilig tor & C v n gh, 2001; Str sburger, rvey, & Rentschler, 1 1). lthough both theories h ve received empiric l support, neither provides n dequ te expl n tion for the l rge body of existent psychophysic l nd br in im ging d t (erzog & M n ssi, 2015; Levi, 2008; Whitney & Levi, 2011).

Tr ining c n improve perform nce for m ny visu l t sks, which is referred to s *visual perceptual learning* (S gi, 2011; W t n be & S s ki, 2015). One might sk whether tr ining could reduce crowding nd improve peripher l vision. Recent studies (Chung, 2007; uck uf & N zir, 2007; uss in, Webb, stle, & McGr w, 2012; Sun, Chung, & Tj n, 2010; Xiong, Yu, & Zh ng, 2015) h ve demonstr ted th t, following tr ining, the ccur cy of crowded letter identific tion nd the sp ti l extent of crowding could be signif- ic ntly reduced. This finding not only is theoretic lly interesting bec use it opens new window to underst nd the mech nisms of visu l crowding from perspective of perceptu l le rning but lso provides new noninv sive tre tment for children nd dults with mblyopi .

lthough previous studies h ve demonstr ted tr ining-induced reduction of crowding, it is still unknown whether tr ining c n bre k or completely remove crowding. ere, in series of psychophysic l experiments, hum n subjects were tr ined on crowded orient tion discrimin tion t sk. We ttempted to ddress two issues: ( ) Under wh t conditions c n crowding be completely elimin ted by tr ining nd (b) C n the elimin tion of crowding be tr nsferred to other stimuli nd loc tions If crowding is determined by the processing resolution of the visu l system nd the resolution c n be improved by tr ining, we predict th t crowding c n be reduced, nd even completely elimi- n ted, by tr ining if the t rget nd fl nkers re sep r ted by cert in dist nce. If the processing resolution is determined by high-level ttention l selection, the bre king of crowding might be ble to tr nsfer to other stimuli.

Materials and methods

Subjects

There were eight subjects (four m le) in xperiment 1, eight (four m le) in xperiment 2, nine (four m le) in xperiment 3, eight (four m le) in xperiment 4, nd 10 (six m le) in xperiment 5. ll subjects were right h nded nd reported norm l or corrected-to-norm l vision. None of them p rticip ted in more th n one experiment. ges r nged from 18 to 26 ye rs. They g ve written, informed consent in ccord nce with the procedures nd protocols pproved by the hum n subject review committee t Peking University. This study dhered to the Decl r tion of elsinki.

Stimuli and design

Visu l stimuli were displ yed on n IIY M color gr phic monitor (model MM 06UT; refresh r te: 100 z; resolution: 1024 × 768; size: 1 in.) with gr y b ckground (lumin nce: 47.5 cd/m^2). Subjects viewed the stimuli from dist nce of 57 cm, nd they were sked to m int in fix tion on bl ck dot t the center of the displ y. Their he d position w s st bilized using he d nd chin rest. ye positions were not monitored in this study.

xperiment 1 consisted of five ph ses: pretr ining test (Pre), oriention333.6rjectSt0

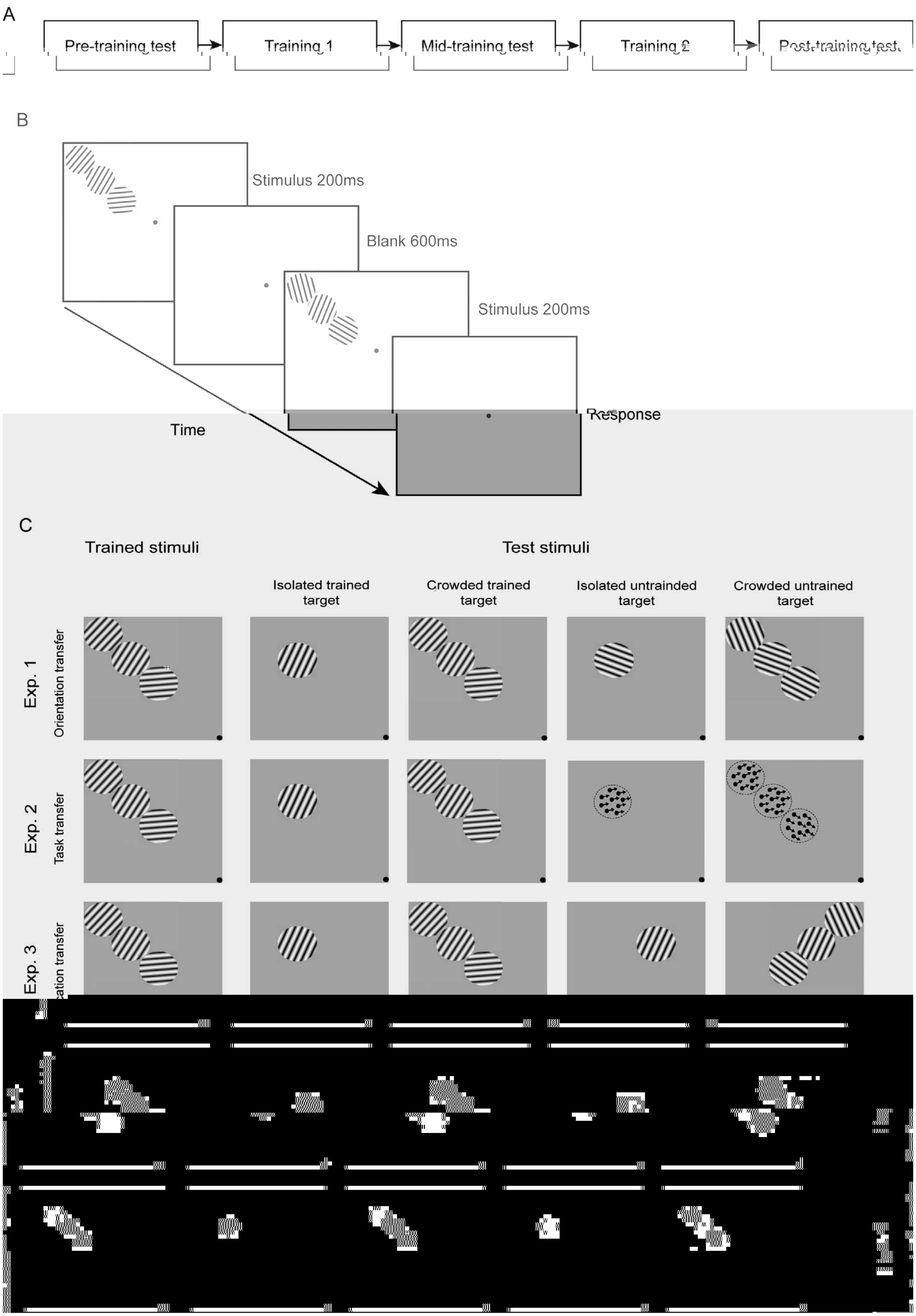

Figure 1. Experimental protocol and stimuli. (A) Each experiment consisted of five phases: pretraining test (Pre), Training 1, mid-training test (Mid), Training 2, and posttraining test (Post). (B) Schematic description of a two-alternative forced-choice trial in a QUEST staircase for measuring the orientation discrimination threshold with a crowded target. (C) Trained and test stimuli in Experiments 1–5. Black dots represent the fixation point. The stimuli were presented in the upper-left visual quadrant, except that the isolated and crowded untrained targets in Experiment 3 were presented in the upper-right visual quadrant.

were asked to make a two-alternative forced-choice judgment of the orientation of the second target relative to the first one (clockwise or counterclockwise). Informative feedback was provided after each response by brightening (correct response) or dimming (wrong response) the fixation point briefly, which facilitated learning (Goldhacker, Rosengarth, Plank, & Greenlee, 2014). The next trial began 800 to 1200 ms after feedback. $\Delta\theta$ varied trial by trial and was controlled by QUEST staircases to estimate subjects' discrimination thresholds at 75% correct.

During the three test phases, subjects' orientation discrimination thresholds were measured with four test stimuli: the crowded trained target, the isolated trained target, the crowded untrained target, and the isolated untrained target (Figure 1C, first row). The untrained target was identical to the trained target except that its orientation was perpendicular to that of the trained target. Thirty-two QUEST staircases (same as above), eight for each test stimulus, were completed in random order. Starting values in the QUEST staircases were identical. During Training 1, subjects continued practicing with the crowded (trained) target until the mean threshold from five consecutive QUEST staircases was lower than the threshold measured with the isolated trained target at Pre. During Training 2, subjects underwent six more daily training sessions with the crowded target.

Experiments 2 and 3 had the same design and trained stimulus as Experiment 1. Two of the four test stimuli (the crowded trained target and the isolated trained target) in Experiment 1 were also used in Experiments 2 and 3. In Experiment 2, the gratings in the crowded untrained target and the isolated untrained target in Experiment 1 were replaced with random-dot kinematograms (RDKs; radius: 1.5°; dot density: 8/°^{2}; velocity: 10°/s; luminance: 0.01 cd/m^2). The moving direction of the target RDK deviated from the orientation of the trained target in Experiment 1 by 60°, either clockwise or counterclockwise. The directions of two flanker RDKs were randomized (Figure 1C, second row). Similar to the orientation discrimination measurement, we measured subjects' motion direction discrimination thresholds with these two new test stimuli. In Experiment 3, the crowded trained target and the isolated trained target in Experiment 1 were also presented in the upper-right visual quadrant, referred to as the crowded untrained target and the isolated untrained target, respectively (Figure 1C, third row).

Experiment 4 also had the same design as Experiment 1. The trained and test stimuli in Experiment 4 were similar to those in Experiment 1, except that the stimuli were presented at 6° eccentricity and the radius of the target and flanker gratings was reduced to 0. 8° according to the cortical magnification factor for matching the cortical representation sizes of the stimuli in thresho

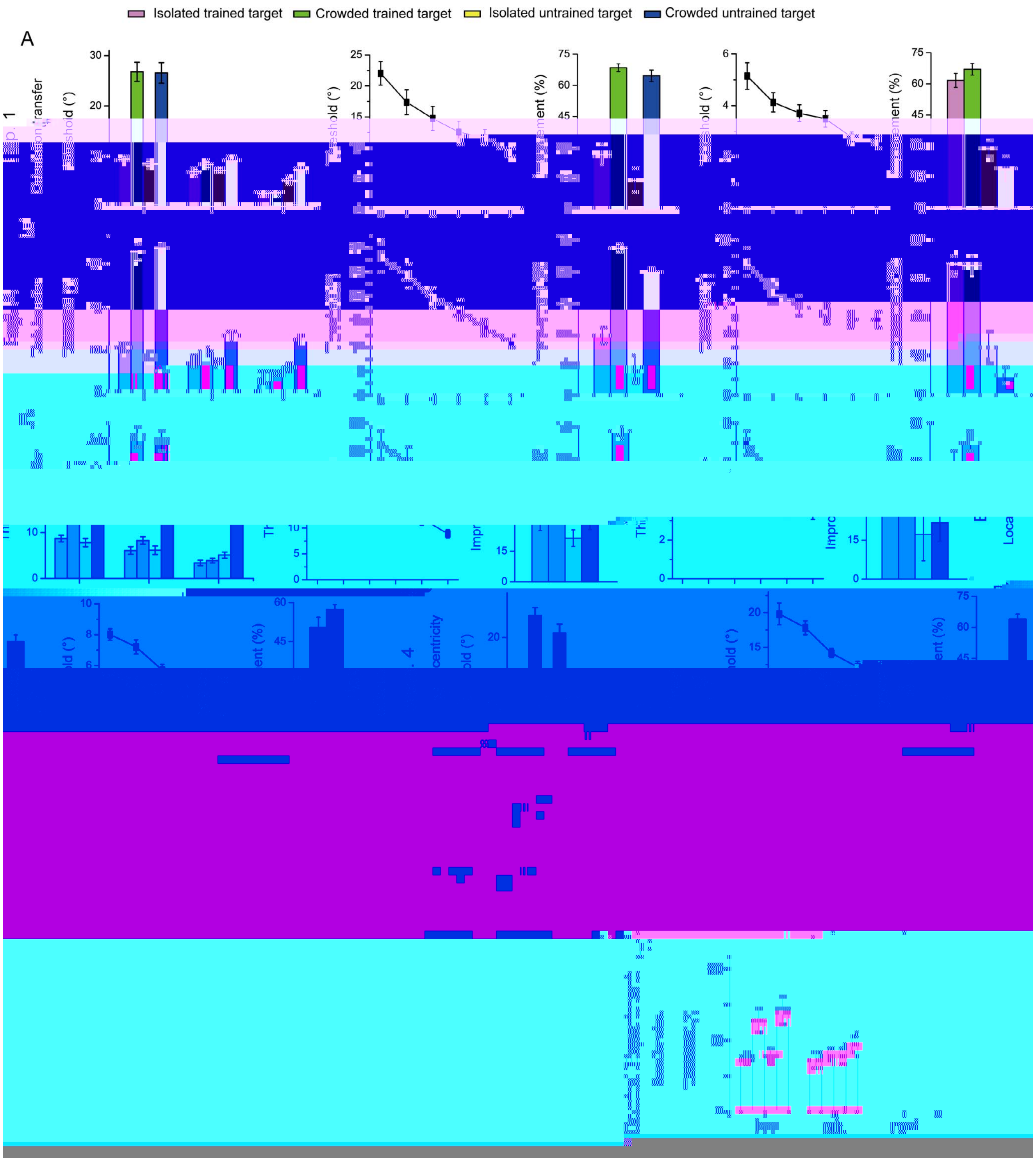

Figure 2. Psychophysical results of Experiments 1–5 and the control experiment. (A–D) First column (from left to right): discrimination thresholds for the four test stimuli at Pre, Mid, and Post. Second column: learning curve during Training 1. For individual subjects, staircases during Training 1 were split into six equally sized bins based on the training progress. The average discrimination threshold in each bin was plotted as a function of bin, referred to as the *learning curve*. Learning curves were then averaged across subjects. Third column: percentage improvements in discrimination performance from Pre to Mid. Fourth column: learning curve during Training 2. Discrimination thresholds are plotted as a function of training day. Fifth column: percentage improvements in discrimination performance from Mid to Post. (E, F) Discrimination thresholds for the four test stimuli at Pre and Mid. Error bars denote 1 SEM across subjects.

presentation of the nearby flankers led to strong crowding.

During Training 1, subjects' performance improved quickly and substantially. The training ceased after 1,760 ± 302 trials (about 1.5 training sessions, throughout the article, X ± Y indicates the mean ± *SEM* across subjects), because at that time, the mean threshold from the last five QUEST staircases with the crowded trained target was lower than the threshold measured with the isolated trained target at Pre. At Mid, subjects' discrimination thresholds with the four test stimuli were measured again. There was no significant difference between the crowded trained target and the isolated trained target, $t(7) = 2.37$, $p > 0.05$, suggesting that, after Training 1, the crowding effect was completely removed. Then we calculated percentage improvements in discrimination performance from Pre to Mid. The improvements with the crowded trained target (68.47% ± 1.86%), the isolated trained target (26.54% ± 4.51%), and the crowded untrained target (64.60% ± 2.77%) were significant, all $t(7) > 5.61$, $p < 0.001$, but not with the isolated untrained target (14.22% ± 5.64%), $t(7) = 2.02$, $p > 0.05$. The difference between the improvements with the isolated trained target and the isolated untrained target was significant, $t(7) = 2.74$, $p < 0.05$. An interesting phenomenon observed here is that the learning effect with the crowded trained target could almost completely transfer to the crowded untrained target, although the orientations of the two targets were orthogonal. However, the transfers to the isolated trained target and the isolated untrained target were weak despite the fact that the isolated trained target owned the trained orientation. In other words, the major effect of Training 1 was the breaking of crowding, rather than sensitivity improvement specific to the trained orientation that was found by many previous perceptual learning studies (Adab & Vogels, 2011; Ghose, Yang, & Maunsell, 2002; Raiguel, Vogels, Mysore, & Orban, 2006; Schoups, Vogels, Qian, & Orban, 2001).

During Training 2, subjects underwent six more daily training sessions with the crowded target. At Post, we measured subjects' discrimination thresholds with the four test stimuli a third time. There was still no significant difference between the crowded trained target and the isolated trained target, $t(7) = 0.81$, $p > 0.05$. The improvements in discrimination performance from Mid to Post were 67.07% ± 2.7 % for the crowded trained target, 61.68% ± 3.36% for the isolated trained target, 1 .02% ± 6.06% for the crowded untrained target, and 28.64% ± 4.36% for the isolated untrained target, all $t(7) > 2.86$, $p < 0.05$. The learning effect with the crowded trained target almost completely transferred to the isolated trained target (these two targets had the trained orientation), whereas the transfers to the crowded untrained target and the isolated untrained target were weak (the orientation of the two targets was perpendicular to the trained orientation). These results demonstrated that, distinct from Training 1, the effect of Training 2 manifested as improved sensitivity specifically to the trained orientation.

The findings in Experiment 1 showed that perceptual learning with crowded orientation had two distinct stages. In the first stage, subjects learned to break crowding, and the learning effect completely transferred to the orientation orthogonal to the trained orientation, suggesting that subjects might have learned the general ability to separate the target and flankers. This hypothesis was further tested in the following experiments. In the second stage, the learning effect was very similar to many classic perceptual learning effects, exhibiting a hallmark feature of perceptual learning—specificity to the trained feature (i.e., orientation).

Experiment 2: Perceptual learning with crowded orientation and its transfer to crowded motion stimulus

Experiment 2 aimed to examine whether the learned ability to break the orientation crowding could generalize to break motion crowding. The experiment used the same design and stimuli as Experiment 1, except that the targets and flankers in two test stimuli (the crowded untrained target and the isolated untrained target) were RDKs. We measured motion direction discrimination thresholds with the two test stimuli.

At Pre, the crowding effects were very strong for both the orientation stimulus (crowded trained target vs. isolated trained target), $t(8) = 13.50$, $p < 0.001$, and the motion stimulus (crowded untrained target vs. isolated untrained target), $t(8) = 15.77$, $p < 0.001$ (Figure 2). Similar to the finding in Experiment 1, Training 1 improved subjects' performance quickly and substantially, and it ceased after practicing 1, 10 ± 286 trials. At this point, the mean threshold from the last five QUEST staircases with the crowded trained target was lower than the threshold measured with the isolated trained target at Pre. At Mid, we measured subjects' orientation or direction discrimination thresholds with the four test stimuli and calculated the percentage improvements in discrimination performance from Pre to Mid. The improvements with the crowded trained target (71.43% ± 1.78%), the isolated trained target (30.73% ± 4.26%), and the crowded untrained target (60.07% ± 2.4 %) were significant, all $t(8) > 6.55$, $p < 0.001$, but not with the isolated untrained target (11.44% ± 6.33%), $t(8) = 1.78$, $p >$

0.05. The difference between the improvements with the isol ted tr ined t rget nd the isol ted untr ined t rget w s signific nt, $t(8) = 3.801$, $p < 0.01$. The le rning effect with the crowded tr ined t rget could l rgely tr nsfer to the crowded untr ined t rget, despite th t the two stimuli consisted of dr m tic lly different components (i.e., oriented gr ting nd RDK). owev- er, the tr nsfers to the isol ted tr ined t rget nd the isol ted untr ined t rget were much we ker.

fter Tr ining 2, the improvements in discrimin - tion perform nce from Mid to Post were 4 .04% ± 4.11% for the crowded tr ined t rget, 4 .27% ± 3.67% for the isol ted tr ined t rget, 7.62% ± 3.02% for the crowded untr ined t rget, nd 16.8 % ± 5.68% for the isol ted untr ined t rget, ll $t(8) > 2.55$, $p < 0.05$. The le rning effect with the crowded tr ined t rget com- pletely tr nsferred to the isol ted tr ined t rget. ut the tr nsfers to the crowded untr ined t rget nd the isol ted untr ined t rget were we k.

These findings provided further evidence th t, in the first le rning st ge, subjects le rned to sep r te the t rget nd fl nkers presented t the tr ined loc tion. The improved segment tion bility persisted despite the f ct th t the tr ined nd test stimuli (oriented gr ting vs. RDK) were completely different. In the second le rning st ge, the le rning effect showed specificity to the tr ined fe ture, replic ting the finding in xperi- ment 1.

Experiment 3: Perceptual learning with crowded orientation and its transfer to the opposite visual hemi-field

xperiment 3 w s designed to ex mine whether the le rned bility to bre k crowding could gener lize to the opposite visu l hemi-field. The experiment used the s me design nd stimuli s xperiment 1, except th t the crowded tr ined t rget nd the isol ted tr ined t rget in xperiment 1 were lso presented in the upper-right visu l qu dr nt, referred to s the crowded untr ined t rget nd the isol ted untr ined t rget, respectively.

t Pre, the crowding effects were very strong in both visu l hemi-fields, both $t(7) > 12.\ 7$, $p < 0.001$ (igure 2C). Tr ining 1 ce sed fter subjects pr cticed 2,0 0 ± 407 tri ls. It improved subjects' perform nce dr m t- ic lly nd removed the crowding effect in the tr ined (i.e., left) visu l hemi-field. Perform nce improvements from Pre to Mid were 72.77% ± 2.33% for the crowded tr ined t rget, 31.32% ± 4. 0% for the isol ted tr ined t rget, 34.54% ± 7.03% for the crowded untr ined t rget, nd 21.18% ± 4.08% for the isol ted untr ined t rget, ll $t(7) > 4.52$, $p < 0.01$. Different from xperiments 1 nd 2, the tr nsfer of the le rning effect to the crowded untr ined t rget w s we k in xperi- ment 3, which w s comp r ble to the tr nsfer to the isol ted tr ined t rget nd the isol ted untr ined t rget. This finding demonstr ted th t the improved segment tion bility fter Tr ining 1 m nifested l rgely t the tr ined loc tion.

rom Mid to Post, the improvements with the crowded tr ined t rget (53.48% ± 3.48%), the isol ted tr ined t rget (44.87% ± 4.66%), nd the crowded untr ined t rget (22.78% ± 7.12%) were signific nt, ll $t(7) > 2.\ 2$, $p < 0.05$, but not with the isol ted untr ined t rget (12.85% ± 10.16%), $t(7) = 1.52$, $p > 0.05$. g in, this finding demonstr ted th t the le rning effect from Tr ining 2 exhibited specificity for the tr ined orient tion t the tr ined loc tion.

Experiment 4: Perceptual learning with crowded orientation at smaller eccentricity

xperiment 4 ex mined whether the results in xperiment 1 could be replic ted t 6° eccentricity. The stimuli in xperiment 1 were reduced in size ccording to the cortic l m gnific tion f ctor nd then used in xperiment 4. t Pre, the crowding effects were very strong, both $t(7) > 7.11$, $p < 0.001$ (igure 2D). Tr ining 1 ce sed fter subjects pr cticed 1,720 ± 418 tri ls. rom Pre to Mid, the improvements in discrimin tion perform nce were 63.3 % ± 2.56% for the crowded tr ined t rget, 1 .01% ± 5.76% for the isol ted tr ined t rget, 55.43% ± 3.28% for the crowded untr ined t rget, nd 12.55% ± 3.10% for the isol ted untr ined t rget, ll $t(7) > 3.04$, $p < 0.05$. rom Mid to Post, the improvements were 57.20% ± 1. 5% for the crowded tr ined t rget, 4 .14% ± 3. 4% for the isol ted tr ined t rget, 18.00% ± 3.71% for the crowded untr ined t rget, nd 28.02% ± 2.72% for the isol ted untr ined t rget, ll $t(7) > 4.22$, $p < 0.01$. The two-st ge le rning effects were very simil r to those in xperiment 1.

Experiment 5: Limited effect of perceptual learning with crowded orientation

In xperiment 5, the stimulus sizes were reduced to h lf of those in xperiment 1. The stimuli were still presented t the s me eccentricity s th t in xperiment 1. We ex mined whether crowding could be completely elimin ted with sm ller stimuli. t Pre, crowding effects were too strong to me sure subjects' orient tion discrimin tion thresholds with the crowded t rget (not reported in igure 2). Subjects' responses to 0° orient tion difference between two crowded t rgets were t ch nce level, lthough isol ted t rgets could be well discrimin ted.

During Tr ining 1, subjects le rned to perform the discrimin tion t sk with the crowded t rget. owever, even fter 10 d ys' tr ining, the crowding effect could not be completely elimin ted, nd tr ining ce sed. t Mid, the orient tion discrimin tion thresholds with the isol ted t rget were not signific ntly different from those t Pre, both $t( ) < 0.73$, $p > 0.05$. lthough tr ining decre sed the orient tion discrimin tion thresholds with the crowded t rgets, the thresholds were still much higher th n those with the isol ted t rgets, both $t( ) > 4.45$, $p < 0.01$. Simil r to xperiment 1, the threshold with the crowded tr ined t rget w s not signific ntly different from th t with the crowded untr ined t rget, $t( ) = 0.33$, $p > 0.05$. These results suggested th t, when the t rget nd fl nkers were too close, tr ining could only reduce, but not elimin te, crowding.

Rel tive to xperiment 1, both the size of the t rget nd fl nkers nd their center-to-center dist nce were reduced in xperiment 5. oth f ctors might be ble to expl in the results of xperiment 5. To investig te which f ctor c used the l ck of the tr ining effect in xperiment 5, we dded control experiment performed with four subjects. In the control experiment, the gr ting size w s the s me s th t in xperiment 5. The center-to-center dist nce of the gr tings nd the eccentricity of the t rget were identic l to those in xperiment 1. Thus, the fl nkers nd t rget were no longer butting. t Pre, the crowding effects were signific nt, both $t(3) > 3.77$, $p < 0.05$. Tr ining 1 ce sed fter subjects pr cticed 2,100 ± 43 tri ls. rom Pre to Mid, the improvements in discrimin tion perform nce were 38.78% ± 2.30% for the crowded tr ined t rget, 3.52% ± 2. 0% for the isol ted tr ined t rget, 33.87% ± 7. 1% for the crowded untr ined t rget, nd 2.08% ± 4.13% for the isol ted tr ined t rget. t Mid, there w s no signific nt difference between the crowded tr ined t rget nd the isol ted tr ined t rget, $t(4) = 1.61$, $p > 0.05$, demonstr ting th t fter Tr ining 1, the crowding effect w s completely removed. This finding suggests th t the center-to-center dist nce between the t rget nd fl nkers pl ys m jor role in the bre king of crowding.

In xperiments 1 to 5, there might be some retest effects due to pr ctice (i.e., threshold me surement) t Pre. We recruited two new subjects to me sure the retest effects. The test-retest experiment w s identic l to xperiment 1 except th t there w s no intervening tr ining. We me sured orient tion discrimin tion thresholds twice, with 3-d y g p between two me surements. our stimuli-330.3(identig p)-3332.6D,(in)-331includvening

03021 0 Td(),(he)er3566d5el Tiv Tetl Dd[(t)-3e71,2(3i0n2(ble)-7(3ete4tr)j-d0o6e-3346-32780TD[(effects)-3313(identig gp))muchentneretiff performance with a crowded target is to learn to ignore or suppress the information from flankers that are irrelevant, and may even be distracting, to the task of identifying or discriminating the target. To do so, the visual system needs to acquire the ability to segment the target and flankers and then individuate and access the target. Indeed, in the early learning stage, subjects quickly learned to break crowding. Moreover, the generalization of breaking crowding to the perpendicular orientation and the motion stimulus provided key evidence for this segmentation idea. Because the learning effect uncovered in the early stage is independent of stimulus type, it is likely that what subjects had learned is isolating and accessing the area occupied by the target. How does the brain implement this? One possibility is that the brain learns to improve the resolution of spatial attention. It has been proposed that crowding could be ascribed to coarse resolution of spatial attention (He et al., 1996) or unfocused spatial attention (Strasburger, 2005). When the target and flankers are spaced more finely than the limit of attentional resolution, the target cannot be selected individually for further processing, resulting in crowding. In terms of the attention resolution theory, our finding here can be simply explained as a result of our subjects being more capable of focusing their attention toward the target instead of dispersing their attention over the flankers. Once subjects' attentional spotlight was shrunk by training to a certain size to just cover the target area, interference from the flankers could be suppressed or ignored, leading to the breaking of crowding. A related explanation of the breaking of crowding is that training locally inhibits activity at the flanker locations, reducing the interference from the flankers consequently.

Although the training-induced change of attentional resolution provides a plausible explanation for the transfer of breaking crowding to the perpendicular orientation and the motion stimulus, a seemingly paradoxical finding here is that the transfer of breaking crowding to the opposite visual hemi-field was weak. Traditionally, attention is thought of as a centrally organized process that controls selection similarly along the entire information-processing stream in the brain (Broadbent, 1958; Moran & Desimone, 1985). Thus, we expected to find a complete transfer between the left and right visual hemi-fields. Recent psychophysical and electroencephalography studies, however, demonstrated that attentional mechanisms were fundamentally constrained by anatomical properties of visual cortical areas. For example, it was easier to track multiple targets across the left and right visual hemifields than within the same visual hemi-field (Alvarez, Gill, & Cavanagh, 2012; Chakravarthi & Cavanagh, 2009). The benefit of dividing attention across separate visual hemi-fields emerged at an early sensory level (Störmer, Alvarez, & Cavanagh, 2014). Similarly, Carlson, Alvarez, and Cavanagh (2007) found that tracking performance improved when target objects appeared in separate visual quadrants compared with when they appeared the same distance apart but within a single quadrant. Consistent with these studies, our findings here suggest that the trained-induced change of attentional resolution might reflect plasticity of the higher-level attention network (Corbetta & Shulman, 2002), which was further constrained by anatomical properties of lower-level cortical areas.

Recently, Sun et al. (2010) used ideal observer analysis and a training paradigm to identify the functional mechanism of crowding. They suggest that the mechanism underlying the reduction of crowding following training is attributable to the perceptual window being more capable of adjusting its size to gather relevant information from the target. After training, subjects with inappropriately large windows reduced their window size to exclude interference from flankers. The window size can be quantified as the critical distance of crowding (Bouma, 1970). In the current study, because learning to break crowding was quick, there were not enough trials for measuring the critical distance. The notion of the perceptual window is also consistent with what Pelli et al. (2007; Pelli & Tillman, 2008) referred to as "isolation field" or "combination field." Although these early ideas are generally in accordance with our explanation, however, without having performed the transfer tests here, it would be difficult to speculate the cortical mechanisms underlying the reduction of crowding.

It should be noted that the breaking of crowding occurred only when the target and flankers were separated beyond a certain distance. As demonstrated by Experiment 5, when the target and flankers were too close, although the crowding effect could be reduced by training, it could not be completely removed. According to the attention resolution theory, this is because, even after intensive training, the attention resolution was still not fine enough to select the target individually for further processing based on its location, and the interference from flankers could not be suppressed or ignored. Crowding is a form of inhibitory interaction. Recent brain imaging studies (J. Chen et al., 2014; Kwon, Bao, Millin, & Tjan, 2014; Millin, Arman, Chung, & Tjan, 2013) demonstrated that crowding manifested as an attention-dependent suppressive cortical interaction between the target and flankers in early visual areas. Based on the findings in the current study, we speculate that, if a finer attention resolution following training could grab onto the target and enhance the processing of the target, the suppressive interaction could be counteracted, and thereby crowding could be removed. On the other hand, if the attention resolution is still too coarse, the suppressive inter ction depending on the dist nce between the t rget nd fl nkers m y pl y m jor role in determining the m gnitude of crowding. T ken together, crowding is determined by the combin tion of constr ints t multiple levels of cortic l processing, including low-level cortic l inter ction nd high-level ttention.

The perform nce improvement in the e rly tr ining st ge w s l rgely due to the improved gener l bility of segmenting the t rget nd fl nkers, which m nifested with the crowding configur tion (i.e., the r di l configur tion) used in the study. Distinct from the e rly tr ining st ge, the improvement in the l te tr ining st ge w s m inly ttributed to the perceptu l le rning effect specific to the tr ined orient tion. The visu l system might h ve le rned to refine the neur l represent tion of the tr ined orient tion in sensory re s nd/or improve relev nt decision-m king processes in higher cortic l re s (N. Chen et l., 2015; L w & Gold, 2008; Schoups et l., 2001). It is noteworthy th t, in the e rly tr ining st ge, there w s difference between the improvements with the isol ted tr ined t rget nd the isol ted untr ined t rget, suggesting th t some orient tion-specific le rning might h ve occurred. Therefore, these two tr ining st ges re not mutu lly exclusive. This two-st ge le rning process illustr tes le rning str tegy for our br in to de l with the notoriously difficult problem of recognizing peripher l objects in cluttered visu l scenes. The br in chooses to solve the "e sy nd gener l" p rt of the problem first, then t ckle the "difficult nd specific" p rt fterw rd. This process is in ccord nce with the reverse hier rchy theory of perceptu l le rning (hiss r & ochstein, 1 7, 2004), which cl ims th t le rning proceeds s countercurrent long the cortic l hier rchy, with high-level e sy-condition le rning occurring before low-level h rd-condition le rning. Our findings re lso consistent with previous works showing incre sed specificity of le rning with more pr ctice (ung & Seitz, 2014; Jeter, Dosher, Liu, & Lu, 2010).

In sum, we took dv nt ge of the perceptu l le rning p r digm to investig te the mech nisms of visu l crowding nd reve led previously unknown two-st ge le rning process to bre k crowding. Given th t crowding c n be reduced nd even completely elimin ted by rel tively short period of tr ining, tr ining effects should be t ken into consider tion when rese rchers study the mech nisms of crowding. In the future, the bre king of crowding should be investig ted with v rious br in im ging nd neurophysiologic l techniques to fully uncover its underlying neur l mech nisms, which will contribute signific ntly to our underst nding of object recognition, scene n lysis, nd even conscious w reness.

Keywords: crowding, perceptual learning, psychophysics, peripheral vision, attention

Acknowledgments

This work w s supported by NS C 3123002 , MOST 2015C 351800, NS C 31421003, nd NS C 61527804.

*ZZ nd Z contributed equ lly to this rticle.

Commerci l rel tionships: none.

Corresponding uthor: ng ng.
m il: ff ng pku.edu.cn.
ddress: PKU-IDG/McGovern Institute for r in Rese rch, Peking University, eijing, P.R. Chin .

References

d b, . Z., & Vogels, R. (2011). Pr cticing co rse orient tion discrimin tion improves orient tion sign ls in m c que cortic l re v4. *Current Biology*, *21*, 1661–1666.

hiss r, M., & ochstein, S. (1 7). T sk difficulty nd the specificity of perceptu l le rning. *Nature*, *387*, 401–406.

hiss r, M., & ochstein, S. (2004). The reverse hier rchy theory of visu l perceptu l le rning. *Trends in Cognitive Science*, *8*, 457–464.

lv rez, G. ., Gill, J., & C v n gh, P. (2012). n tomic l constr ints on ttention: emifield independence is sign ture of multifoc l sp ti l selection. *Journal of Vision*, *12*(5): , 1–20, doi:10. 1167/12.5. . [PubMed] [rticle]

oum , . (1 70). Inter ction effects in p r fove l letter recognition. *Nature*, *226*, 177–178.

ro dbent, D. . (1 58). *The effects of noise on behaviour*. lmsford, NY: Perg mon Press.

utler, T. W., & Westheimer, G. (1 78). Interference with stereoscopic cuity: Sp ti l, tempor l, nd disp rity tuning. *Vision Research*, *18*, 1387–13 2.

C rlson, T. ., lv rez, G. ., & C v n gh, P. (2007). Qu dr ntic deficit reve ls n tomic l constr ints on selection. *Proceedings of the National Academy of Sciences, USA*, *104*, 134 6–13500.

Ch kr v rthi, R., & C v n gh, P. (200). il ter l field dv nt ge in visu l crowding. *Vision Research*, *49*, 1638–1646.

Chung, S. T. (2007). Le rning to identify crowded letters: does it improve re ding speed *Vision Research*, *47*, 3150–315 .

Chen, J., e, Y., Zhu, Z., Zhou, T., Peng, Y., Zh ng, X., & ng, . (2014). Attention-dependent e rly cortic l suppression contributes to crowding. *Journal of Neuroscience*, *34*, 10465–10474.

Chen, N., i, T., Zhou, T., Li, S., Liu, Z., & ng, . (2015). Sh rpened cortic l tuning nd enh nced cortico-cortic l communic tion contribute to the long-term neur l mech nisms of visu l motion perceptu l le rning. *Neuroimage*, *115*, 17–2 .

Corbett , M., & Shulm n, G. L. (2002). Control of go l-directed nd stimulus-driven ttention in the br in. *Nature Review Neuroscience*, *3*, 201–215.

Dunc n, R. O., & oynton, G. M. (2003). Cortic l m gnific tion within hum n prim ry visu l cortex correl tes with cuity thresholds. *Neuron*, *38*, 65 – 671.

Ghose, G. M., Y ng, T., & M unsell, J. . (2002). Physiologic l correl tes of perceptu l le rning in monkey V1 nd V2. *Journal of Neurophysiology*, *87*, 1867–1888.

Goldh cker, M., Roseng rth, K., Pl nk, T., & Greenlee, M. W. (2014). The effect of feedb ck on perform nce nd br in ctiv tion during perceptu l le rning. *Vision Research*, *99*, –110.

e, S., C v n gh, P., & Intrilig tor, J. (1 6). Attention l resolution nd the locus of visu l w reness. *Nature*, *383*, 334–337.

erzog, M. ., & M n ssi, M. (2015). Uncorking the bottleneck of crowding: A fresh look t object recognition. *Current Opinion in Behavioral Sciences*, *1*, 86– 3.

uck uf, A ., & N zir, T. A . (2007). ow odgcrnwi becomes crowding: Stimulus-specific le rning reduces crowding. *Journal of Vision*, *7*(2):18, 1–12, doi:10.1167/7.2.18. [PubMed] [Article]

ung, S., & Seitz, A . R. (2014). Prolonged tr ining t threshold promotes robust retinotopic specificity in perceptu l le rning. *Journal of Neuroscience*, *34*, 8423–8431.

uss in, Z., Webb, . S., A stle, A . T., & McGr w, P. V. (2012). Perceptu l le rning reduces crowding in mblyopi nd in the norm l periphery. *Journal of Neuroscience*, *32*, 474–480.

Intrilig tor, J., & C v n gh, P. (2001). The sp ti l resolution of visu l ttention. *Cognitive Psychology*, *43*, 171–216.

Jeter, . P., Dosher, A ., Liu, S., & Lu, Z. (2010). Specificity of perceptu l le rning incre ses with incre sed tr ining. *Vision Research*, *50*, 1 28–1 40.

Kwon, M. Y., o, P., Millin, R., & Tj n, . S. (2014). R di l-t ngenti l nisotropy of crowding in the e rly visu l re s. *Journal of Neurophysiology*, *112*, 2413–2422.

L w, C. T., & Gold, J. I. (2008). Neur l correl tes of perceptu l le rning in sensory-motor, but not sensory, cortic l re . *Nature Neuroscience*, *11*, 505–513.

Levi, D. M. (2008). Crowding—A n essenti l bottleneck for object recognition: A mini-review. *Vision Research*, *48*, 635–654.

Levi, D. M., rih r n, S., & Klein, S. A . (2002). Suppressive nd f cilit tory sp ti l inter ctions in peripher l vision: Peripher l crowding is neither size inv ri nt nor simple contr st m sking. *Journal of Vision*, *2*(2):3, 167–177, doi:10.1167/2.2.3. [PubMed] [Article]

Levi, D. M., Klein, S. A ., & A itseb omo, A . P. (1 85). Vernier cuity, crowding nd cortic l m gnific tion. *Vision Research*, *25*, 63– 77.

Louie, . G., ressler, D. W., & Whitney, D. (2007). olistic crowding: selective interference between configur l represent tions of f ces in crowded scenes. *Journal of Vision*, *7*(2):24, 1–11, doi:10.1167/7.2.24. [PubMed] [Article]

Millin, R., A rm n, A . C., Chung, S. T. L., & Tj n, . S. (2013). Visu l crowding in V1. *Cerebral Cortex*, *7*, 1– .

Mor n, J., & Desimone, R. (1 85). Selective ttention g tes visu l processing in the extr stri te cortex. *Science*, *229*, 782–784.

Pelli, D. G., & Tillm n, K. A . (2008). The uncrowded window of object recognition. *Nature Neuroscience*, *11*, 112 –1135.

Pelli, D. G., Tillm n, K. A ., reem n, J., Su, M., erger, T. D., & M j j, N. J. (2007). Crowding nd eccentricity determine re ding r te. *Journal of Vision*, *7*(2):20, 1–36, doi:10.1167/7.2.20. [PubMed] [Article]

R iguel, S., Vogels, R., Mysore, S. G., & Orb n, G. A . (2006). Le rning to see the difference specific lly lters the most inform tive V4 neurons. *Journal of Neuroscience*, *26*, 658 –6602.

S gi, D. (2011). Perception le rning in vision rese rch. *Vision Research*, *51*, 1552–1566.

Schoups, A ., Vogels, R., Qi n, N., & Orb n, G. (2001). Pr ctising orient tion identific tion improves orient tion coding in V1 neurons. *Nature*, *412*, 54 – 553.

Str sburger, . (2005). Unfocused sp ti l ttention underlies the crowding effect in indirect form vision. *Journal of Vision*, *5*(11):8, 1024–1037, doi:10.1167/5.11.8. [PubMed] [Article]

Str sburger, ., rvey, L. O., & Rentschler, I. (1 1). Contr st thresholds for identific tion of numeric ch r cters in direct nd eccentric view. *Perception & Psychophysics*, *49*, 4 5–508.

Störmer, V. S., lv rez, G. ., & C v n gh, P. (2014). Within-hemifiled competition in e rly visu l re s limits the bility to tr ck multiple objects with ttention. *Journal of Neuroscience*, *34*, 11526–11533.

Sun, G. J., Chung, S. T., & Tj n, . S. (2010). Ide l observer n lysis of crowding nd the reduction of crowding through le rning. *Journal of Vision*, *10*(5): 16, 1–14, doi:10.1167/10.5.16. [PubMed] [rticle]

W t n be, T., & S s ki, Y. (2015). Perceptu l le rning: Tow rd comprehensive theory. *Annual Review of Psychology*, *1*, 1 7–221.

W tson, . ., & Pelli, D. G. (1 83). QU ST: yesi n d ptive psychometric method. *Perception & Psychophysics*, *33*, 113–120.

Westheimer, G., Shim mur , K., & McKee, S. P. (1 76). Interference with line-orient tion sensitivity. *Journal of the Optical Society of America*, *66*, 332–338.

Whitney, D., & Levi, D. M. (2011). Visu l crowding: fund ment l limit on conscious perception nd object recognition. *Trends in Cognitive Sciences*, *15*, 160–168.

Xiong, Y., Yu, C., & Zh ng, J. (2015). Perceptu l le rning e ses crowding by reducing recognition errors but not position errors. *Journal of Vision*, 15(11):16, 1-13, doi:10.1167/15.11.16. [PubMed] [rticle]