Rapid and long-lasting reduction of crowding through training

Amit Yashar Department of Psychology, New York University, New York, NY, USA

Jiageng Chen Department of Psychology, New York University, New York, NY, USA

Marisa Carrasco Department of Psychology and Center for Neural Sciences, New York University, NY, USA

Crowding is the failure to identify an object in the peripheral visual field in the presence of nearby objects. Recent studies have shown that crowding can be alleviated after several days of training, but the processes underlying this improvement are still unclear. Here we tested whether a few hundred trials within a short period of training can alleviate crowding, whether the learning is location specific, and whether the improvement reflects facilitation by target enhancement or flankers suppression. Observers were asked to identify the orientation of a letter in the periphery surrounded by two flanker letters. Observers were tested before (pretest) and after (posttest) training (600 trials). In Experiment 1 we tested whether learning is location specific or can transfer to a different location; the training and test occurred at the same or different hemifields. In a control experiment, we ruled out alternative explanations for the learning effect in Experiment 1. In Experiment 2, we assessed different components of feature selection by training with either the same flanker polarity as the pre/posttest but opposite polarity group (flanker polarity group) or the same target polarity as the pre/posttest but opposite flanker polarity (target polarity group). Following training, overall performance increased in all four conditions, but only the same-location group (Experiment 1) and the same flanker polarity (Experiment 2) showed a significant reduction in crowding as assessed by the distance at which the flankers no longer interfere with target identification, that is, the critical spacing. These results show that training can rapidly reduce crowding and that improvement primarily reflects learning to ignore the irrelevant flankers. Remarkably, in the two conditions in which training significantly reduced crowding, the benefit of short training persisted for up to a year.

Introduction

We tend to believe that we have a continuous and detailed representation of the visual environment. However, we realize that this is an illusion when we are asked to find a target among distractors in visual search or to scrutinize an object in the periphery. These processing limitations are usually attributed to the well-known decline in visual acuity in the periphery (Anton-Erxleben & Carrasco, 2013; Strasburger, Rentschler, & Jüttner, 2011). However, much of the impediment of detecting, discriminating, or localizing a target in the periphery is due to the phenomenon of crowding—that is, the failure to identify an object when it is presented along nearby objects (flankers), but not when it is presented alone (e.g., Bouma, 1970; Levi, 2008; Pelli, Palomares, & Majaj, 2004; Pelli & Tillman, 2008; Whitney & Levi, 2011). For example, you can identify a book on your shelf without looking at it directly, but it is a lot more difficult to recognize it when other books surround it. Crowding occurs for target identification but almost never for target detection (Pelli et al., 2004). It is assumed that to recognize an object two stages of processing are required: first, detecting the object's features, and second, integrating the features into a coherent object (e.g., Pelli, Burns, Farell, & Moore-Page, 2006; Suchow & Pelli, 2013). For example when identifying the letter *T*, we first detect the horizontal and the vertical lines elements (the features) and then we combine the horizontal line above the vertical one (correct integration).

The conditions required for crowding are well established. Mainly, the critical spacing—that is, the minimal space between the target and the flankers that permits identification performance similar to when no flankers are presented—increases with eccentricity of

Citation: Yashar, A., Chen, J., & Carrasco, M. (2015). Rapid and long-lasting reduction of crowding through training. *Journal of Vision*, *15*(10):15, 1–15, doi:10.1167/15.10.15.

doi: 10.1167/15.10.15 Received March 31, 2015; published November 19, 2015 ISSN 1534-7362

the target object (e.g., Pelli et al., 2004) and with similarity between the target and the flankers (e.g., Chung, Levi, & Legge, 2001; Kooi, Toet, Tripathy, & Levi, 1994). It has been proposed that crowding creates assimilation or averaging of the target and the flankers' signals (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001), and affects appearance in the sense that a crowded object tends to take characteristics of the flankers (Greenwood, Bex, & Dakin, 2010). Thus, some consider that crowding is simply texture perception "when we do not wish it to occur" (Parkes et al., 2001, p. 742; for a review, see Whitney & Levi, 2011).

Given the important role of object identification in the periphery for reading, driving, and almost any interaction with the visual environment for both neurotypical and atypical populations, the motivation of understanding how to alleviate the effect of crowding is clear and pressing. Crowding has important clinical implications for patients with macular degeneration, amblyopia, and dyslexia (e.g., Bonneh, Sagi, & Polat, 2007; Chung, Li, & Levi, 2012; Hussain, Webb, Astle, & McGraw, 2012; Polat, 2008; for a review, see Whitney & Levi, 2011). Moreover, understanding how to alleviate the effects of crowding can shed new light on the processes underlying crowding itself. In the last decades a growing number of studies have investigated the role of training in improving basic perceptual tasks, a phenomenon known as perceptual learning. Training increases performance on various stimuli and tasks including contrast discrimination and detection (e.g., Dosher & Lu, 1999; Fiorentini & Berardi, 1981; Mukai et al., 2007), spatial acuity (e.g., Poggio, Fahle, & Edelman, 1992), orientation discrimination (e.g., Schoups, Vogels, & Orban, 1995; Szpiro, Wright, & Carrasco, 2014),x motion detection (e.g., X. Wang, Zhou, & Liu, 2013; Watanabe, Náñez, & Sasaki, 2001), motion discrimination (e.g., Szpiro, Spering, & Carrasco, 2014), face identification (e.g., Husk, Bennett, & Sekuler, 2007), texture discrimination (e.g., Harris, Gliksberg, & Sagi, 2012; Karni & Sagi, 1991), and target detection in visual search (e.g., Ahissar & Hochstein, 1997; Carrasco, Ponte, Rechea, & Sampedro, 1998; Frank et al., 2013).

Studies have shown that prolonged training ($\geq$6 days and more) improves the identification of a target under crowded conditions (Chung, 2007; Chung et al., 2012; Hussain et al., 2012), and that training induced improvement can occur within the first session (Chung, 2007). But it is unknown whether the initial learning is procedural or perceptual, for how long the learning persists, whether the learning is target-driven or flanker-driven, and what the mechanisms are that underlie fast learning. Short training (between dozens to hundreds of trials) has been found to improve perception in basic perceptual tasks and stimuli, such as contrast discrimination of compound spatial frequency (Fiorentini & Berardi, 1981; Mukai et al., 2007) and vernier acuity (Poggio et al., 1992). Using a letter stimulus that consists of spatial combination of Gabor elements, Suchow and Pelli (2013) reported a double dissociation between feature detection (i.e., detecting the Gabors) and feature spatial combination (identifying the letter) during perceptual training, and showed that combination learning is faster than detection learning. Based on the finding that combination learning is fast, we tested the following hypothesis: If crowding reflects a failure of the integration process, then short training should substantially reduce the critical spacing.

In the present study, we used a well-established crowding procedure to assess whether fast improvement under crowding is location specific (Experiment 1) and whether the reduction of critical spacing reflects facilitation of either target- or flanker-related processes (Experiment 2). Moreover, we investigated whether for those conditions for which training significantly reduces crowding, the benefit would still be there 8–12 months after training.

Experiments

Experiment 1

We tested whether crowding's critical spacing can be reduced with short training. Observers were asked to discriminate the orientation of the letter *T* presented in the periphery along with two vertical flankers. Observers were trained under crowded conditions for 600 trials using a staircase procedure. Before and after training observers were tested with six different distances between target and flankers. We compared changes in overall accuracy and in critical spacing between the pretest and the posttests. In one group of observers the stimuli during training and test were presented in the same location (same-location group), whereas in another group of observers the stimuli was presented in a different location between training and test (different-location group). Were learning location specific, we would expect to find learning only in the same-location group. Alternatively, were learning to transfer completely, we would expect to find the same extent of learning in both groups. Last, were learning to transfer partially, we would expect to find less learning in the different-location group than the same-location group.

Method

Observers: Twenty-two New York University male and female undergraduate students participated for course credit. All reported having normal or corrected-to-normal visual acuity and normal color vision. The University Committee on Activities Involving Human Subjects at New York University approved experimental procedures.

Apparatus: Observers were tested individually in a dimly lit room. An Intel Core 2 Duo computer connected to a 21-in CRT monitor (SONY CPD-G520, with 1280 × 960 resolution and 90-Hz refresh rate). Stimuli were programmed in Matlab (The MathWorks, Inc., Natick, MA) and MGL (http://gru.stanford.edu/doku.php/mgl/overview). Responses were collected via the computer keyboard. A chin-rest set the 57-cm viewing distance. Eye movements were recorded by an Eyelink 1000 (SR Research) infrared eye tracker.

Stimuli: Sample stimulus displays are presented in Figure 1a. All stimuli were presented on a gray background (50 cd/m^2). The fixation display was a black (0.16 × 0.16 degrees of visual angle [dva]) cross sign (+) in the center of the screen. The crowding display consisted of the fixation cross along with three letters: a target and two flankers. The target was the capital letter *T* oriented upright, inverted, or tilted 90- to the left or to the right (Figure 1a). Flankers were capital *H*s, either upright or with a 90° tilt, positioned one above and one below the target. Both target and flankers subtended 1 × 1 dva. The target was presented at 9 dva eccentricity on the horizontal meridian. Target and flanker color were black (0.5 cd/m) for 12 observers and white (100 cd/m^2) for the other observers, such that the luminance contrast between the letters and the background was 0.98 and 0.33, respectively.

Procedure: We followed a procedure used in several crowding studies (e.g., Grubb et al., 2013; Rashal & Yeshurun, 2014; Scolari, Kohnen, Barton, & Awh, 2007; Yeshurun & Rashal, 2010). Each trial began with the presentation of the fixation display. Once the observer fixated for 250 ms, then the crowding display was presented for 30 ms (20 ms for one observer because his performance was at ceiling at 30 ms). After 500 ms of response delay, observers had to report the orientation of the target by pressing one of four designated keys (8, 5, 4, or 6 for upward, downward, left, and right, respectively). Observers were instructed to respond as accurate as possible without speed stress.

Design: A 1-hr session consisted of a pretest phase of 180 trials followed by a training phase of 600 trials and a posttest phase of 180 trials. During pre- and posttest the center-to-center distance between target and flankers varied randomly between 1.5, 2.0, 2.5, 3.0, 4.0, and 5.0 dva. During training the center-to-center distance was adjusted with a three-up one-down staircase rule (Levitt, 1971), and correct and incorrect responses were followed by a high or low feedback tone, respectively. There were two training groups (Figure 1b). In the same-location group, the target and flankers were to the right of fixation both during training and tests blocks, whereas in the different-location group, the target and flankers were to the right of fixation during the tests blocks, but to the left of fixation during the training blocks (i.e., on the other hemifield). Each experiment began with 30 practice trials with a longer display duration (70 ms).

Results

Critical spacing: Mean accuracies as function of distance for each group are presented in Figure 2. For each participant and condition, we modeled the effect of target–flanker distance on accuracy with the following exponential function (following Grubb et al., 2013; Rashal & Yeshurun, 2014; Scolari et al., 2007; Yeshurun & Rashal, 2010).

$$pc = a\left(1 - e^{(-s(d-i))}\right) \tag{1}$$

where *pc* is proportion correct, *a* is the asymptote, *s* is the scaling factor, *d* is the target–flanker distance, and *i* is the *x*-intercept. The asymptotic value, scaling factor, and *x*-intercept were adjusted using nonlinear least-squares fitting method (with a Trust-Region algorithm provided in Matlab Curve Fitting Toolbox). The critical spacing *c* was defined as the target–flanker distance at which accuracy achieved 90% of the asymptotic value, and it was calculated using the following equation:

$$c = i - \frac{\ln(0.1)}{s} \tag{2}$$

The coefficient of determination (R^2; adjusted to the degrees of freedom) was used to assess how well the model fit the data. The average R^2 for individual fits was 86% ($SE = 1.7\%$). Observers whose R^2 *z*-score was ≤ -3 were replaced so that each group had 11 observers. The fitted model along with mean accuracy as a function of target distance for pre- and posttest in each group are depicted in Figure 2. An example of this estimation for one participant is presented in Figure 3, left panel. Mean critical spacing for the different groups are presented in Table 1.

An ANOVA with learning (pre- vs. posttest) as within-subjects and training group (same location vs. different location) as between-subjects was conducted on critical spacing. The main effect of group was not significant, $F < 1$. The main effect of learning on critical spacing was significant, $F(1, 20) = 10.67$, $p < 0.004$. This effect did not interact with group, $F(1, 20) = 1.78$, $p > 0.1$. However, based on the well-known location specificity of perceptual learning, we conducted preplanned tests of the magnitude of learning for each group. We calculated the change in critical spacing by subtracting the posttest critical spacing from the pretest, such that a score of zero indicates no learning (Figure 4). A one-sample *t* test between the

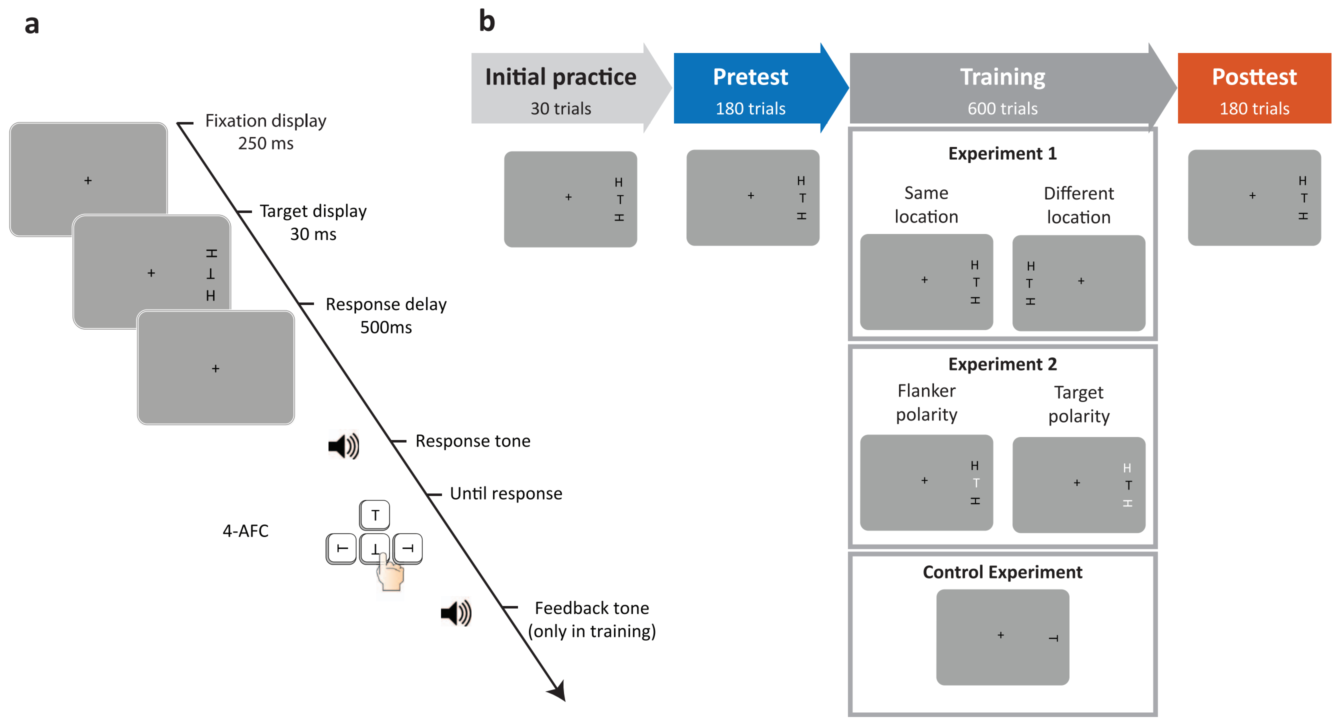

Figure 1. Illustration of the procedure and design of Experiment 1, the control experiment, and Experiment 2. (a) An example of the sequence of events within a trial in all experiments. (b) Examples of stimulus for the training and tests for the same-location and different-location groups in Experiment 1, the flankers-polarity and target-polarity groups in Experiment 2, and the control experiment.

critical spacing change and zero revealed a significant effect of learning on critical spacing in the same-location group, $t(10) = 4.21$, $p < 0.0001$, but not in the different-location group, $t(10) = 1.16$, $p > 0.1$. A scatterplot (Figure 5a) with the data for the individual observers shows that whereas all observers in the same-location group showed reduction of the critical spacing between the pre- and posttest, over a third of the observers in the different-location group did not show reduction.

We also estimated the critical spacing using a two-line method (e.g., Chung, 2002; Chung et al., 2001; Levi, Song, & Pelli, 2007; Pelli et al., 2004; Yeshurun & Rashal, 2010). For each participant and condition, we modeled the effect of target–flanker distance on accuracy using two straight lines. The first line had a positive slope that indicates the interference effect as a function of target–flanker distance, and the second line had a slope of zero that indicates the asymptotic level of performance. The critical spacing is the intersecting point between the two lines (Figure 2, right panel). An example of this estimation for one participant is presented in Figure 3, right panel. The average adjusted R^2 was 80% ($SE = 3\%$). The pattern of results is similar to that of the first model. The critical spacing was reduced only in the same-location group $t(10) = 2.98$, $p < 0.007$, but not in the different location group, $t(10) = 1.01$, $p > 0.1$. Mean critical spacing is presented in Table 1.

Accuracy: A ($6 \times 2 \times 2$) three-way ANOVA was conducted with target–flanker distance (1, 1.5, 2, 3, 4, and 5 dva) and learning (pre- and posttest) as within-subjects conditions and group (same location vs. different location) as between-subjects conditions. The main effects of learning as well as distance were significant, $F(1, 20) = 26.74$, $p < 0.0001$, and $F(5, 100) = 155.38$, $p < 0.0001$, respectively. The main effect of group was not significant $F(1, 20) = 0.52$, $p > 0.1$. Neither the three-way interaction nor the two-way interactions were significant, $F < 1$; the only marginal interaction was that of learning *X* distance, $F(5, 100) = 1.97$, $p = 0.09$, which indicated that learning decreased as a function of target–flanker distance.

The present results show that a short session of training can induce substantial improvement in target identification under crowded conditions. The reduction of the critical spacing in the same-location group, which reflects mainly improved performance in the smaller target to flankers distances (as indicated in Figure 2), implies that the effect cannot be attributed to procedural learning, which would predict an overall

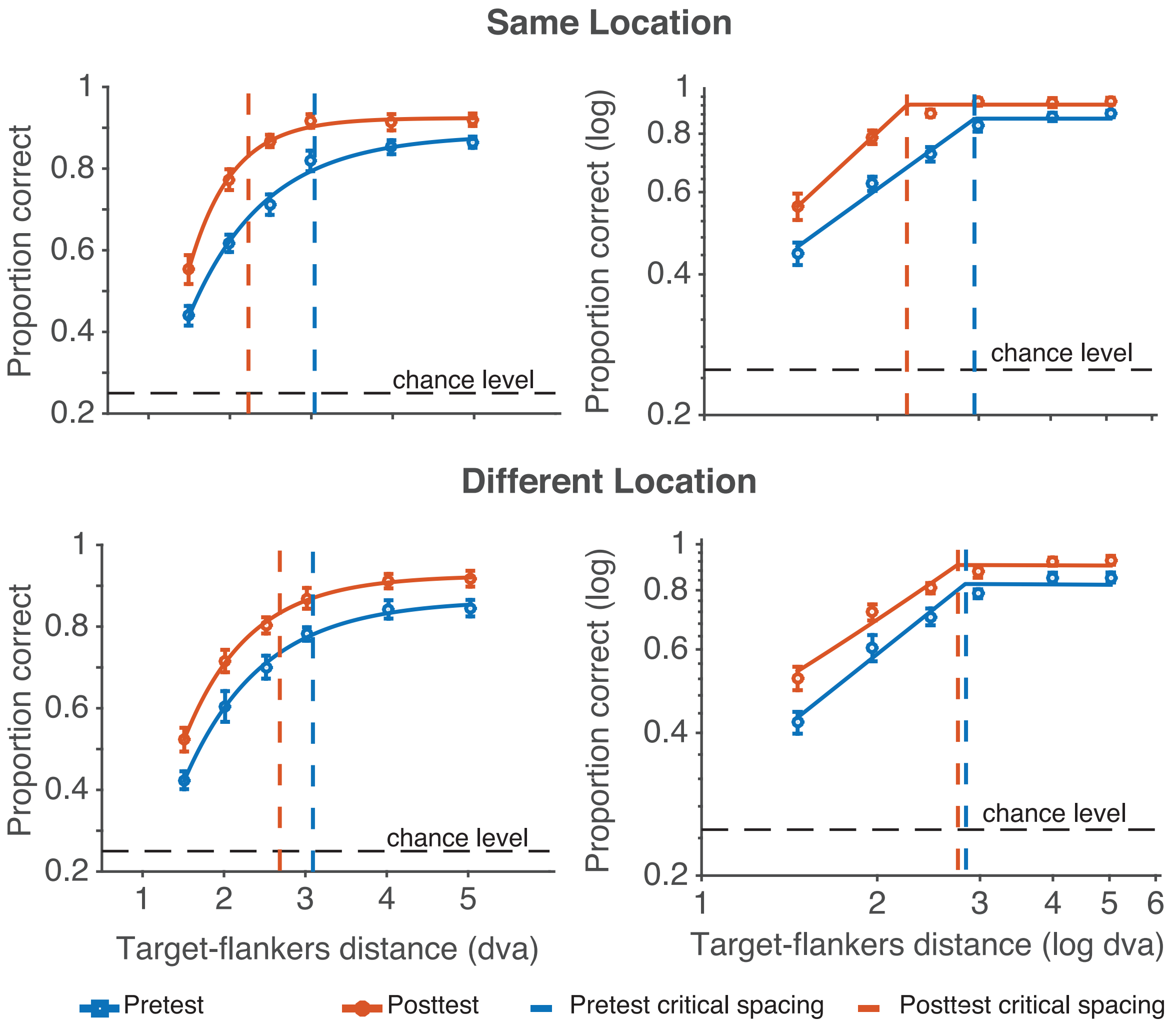

Figure 2. Mean proportion correct as a function of target–flankers distance in dva for pre- and posttests in Experiment 1, for same-location group (top panels) and (b) different-location group (bottom panels). For each group we plotted proportion correct as a function of target–flankers distance along with the exponential curve model (left panels) and two-line fitting method (right panels). Error bars correspond to ±1 *SE*. Dashed lines indicate the estimated critical spacing for each group. The two-line fitting was plotted with log–log axes. The adjusted R^2 for the fitting are 0.99, 0.96, 0.96, and 0.95 for the top-left, bottom-left, top-right, and bottom-right panels, respectively.

improvement across all distances and full transfer between the locations. The effect on critical spacing did not interact with group. However, when we analyzed the effect separately for each group we find learning only in the same-location group. This finding suggests that although some learning transferred to the other location, learning was more pronounced at the trained location. Several papers have stated that transfer is not an all-or-none process, but rather there are degrees of transfer. Indeed, several transfer indices have been applied to characterize partial transfer (e.g., Ahissar & Hochstein, 1997; Jeter, Dosher, Petrov, & Lu, 2009; Lu, Chu, Dosher, & Lee, 2005; R. Wang, Zhang, Klein, Levi, & Yu, 2014).

Control experiment

The results of Experiment 1 show a rapid and substantial improvement in the discrimination of the flanked target and a decrement in the critical spacing for the same-location group. Even though the two following alternative explanations would have predicted similar improvement across distances, we conducted a control experiment to rule out their possible contribution: (a) The improvement merely reflected procedural learning, that is, observers simply learned the response demands of the task (e.g., Beaunieux et al., 2006; Cohen & Squire, 1980; Fahle & Poggio, 2002); or (b) training facilitated the perception of the rapidly presented targets per se (30 ms). In this experiment,

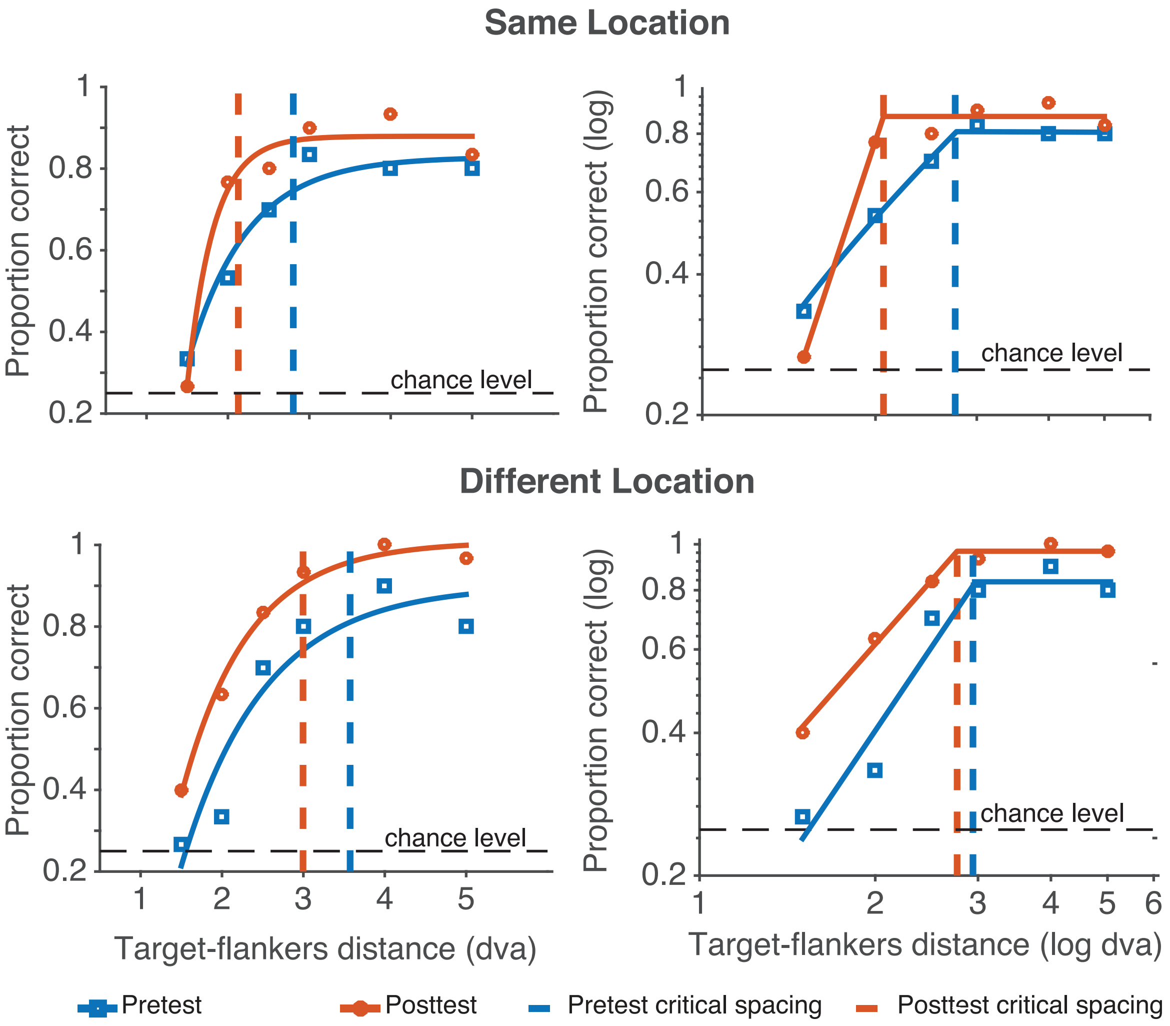

Figure 3. Two sample observers: one for the same-location group (top panels) and one for the different-location group (bottom panels). For each observer we plotted proportion correct as a function of target–flankers distance along with the exponential curve model (left panels) and two-line fitting method (right panels). Dashed lines indicate the estimated critical spacing for each observer. The two-line fitting was plotted with log–log axes. The adjusted R^2 for the fitting are 0.94, 0.89, 0.96, and 0.95 for the top-left, bottom-left, top-right, and bottom-right panels, respectively.

observers trained without the flankers, that is, only the target was displayed. Had observers learned the response demands of the task and/or the perception of rapidly displayed targets, then training with uncrowded displays should still improve performance in the crowded display (at posttest).

Method

Observers: Nine New York University undergraduate male and female students participated for course credit. All reported having normal or corrected-to-normal visual acuity and normal color vision.

		Experiment 1			Experiment 2	
Fitted models	Test	Same location	Different location	Control experiment	Flanker-polarity	Target-polarity
Exponential curve	Pretest	3.37 (.33)	3.33 (.42)	3.27 (.36)	3.21 (.28)	2.62 (.25)
	Posttest	2.30 (.20)	2.88 (.27)	3.38 (.57)	2.27 (.24)	2.72 (.21)
Two-line method	Pretest	3.17 (.20)	3.22 (.32)	3.19 (.26)	2.91 (.11)	2.60 (.19)
	Posttest	2.53 (.12)	2.84 (.23)	3.02 (.39)	2.47 (.18)	2.87 (.19)

Table 1. Mean critical spacing for the pre- and posttest in each group in Experiment 1, the control experiment, and Experiment 2. *Notes*: Standard error in parentheses.

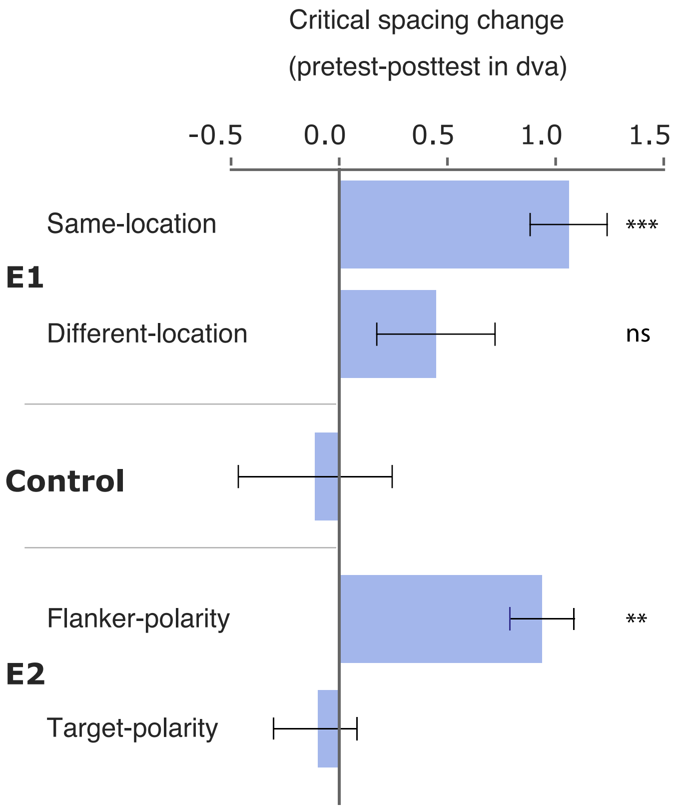

Figure 4. Mean difference between the pre- and posttest of the critical spacing as calculated by the exponential curve model for same-location and different-location groups in Experiment 1, control experiment, and flanker-polarity and target-polarity groups in Experiment 2. Error bars correspond to ±1 *SE*. $^{**}p <$ 0.01, $^{***}p < 0.0001$.

Stimuli and procedure: The stimuli procedure and design were the same as those in Experiment 1 same-location group except for the following: (a) During training the target was presented alone, and (b) during pre- and posttest, in addition to the six target-to-flankers distances, there were 30 trials with no flankers (210 trials for each test). Illustration of the training and pre- and posttests are depicted in Figure 1b.

Results

Critical spacing: The average adjusted R^2 was 87% ($SE = 2.6\%$). Mean accuracy as a function of target spacing for pre- and posttest is depicted in Figure 6a. Paired comparison between pre- and posttests was conducted on critical spacing. Training did not affect the critical spacing, $F < 1$ (Figure 4). For the two-line fit model, the average adjusted R^2 was 83% ($SE = 4\%$). There was no learning effect on the critical spacing with this fit either ($t < 1$). Mean critical spacing is presented in Table 1.

Accuracy: A (6 × 2) two-way ANOVA was conducted with learning (pre- and posttest) and target–flankers spacing (1.5, 2, 2.5, 3, 4, and 5 dva) as within subject conditions. The main effect of spacing was significant, $F(6, 48) = 73.35$, $p < .0001$. However, neither the main effect of learning nor its interaction with spacing was significant ($F < 1$). Figure 6b illustrates that throughout the five training blocks, performance for the target presented alone was ≥95%.

The results of the control experiment suggest that perceptual learning underlies the improvement in Experiment 1. In the control experiment observers were trained with the same stimulus and procedure but without the flankers. The fact that performance was very high during training and did not improve between pre- and posttest indicates that there was no need for procedural learning after the initial 30 practice trials (before pretest).

Experiment 2

In this experiment we examined what are the processes that underlie the fast learning shown in Experiment 1. Specifically we tested whether training in

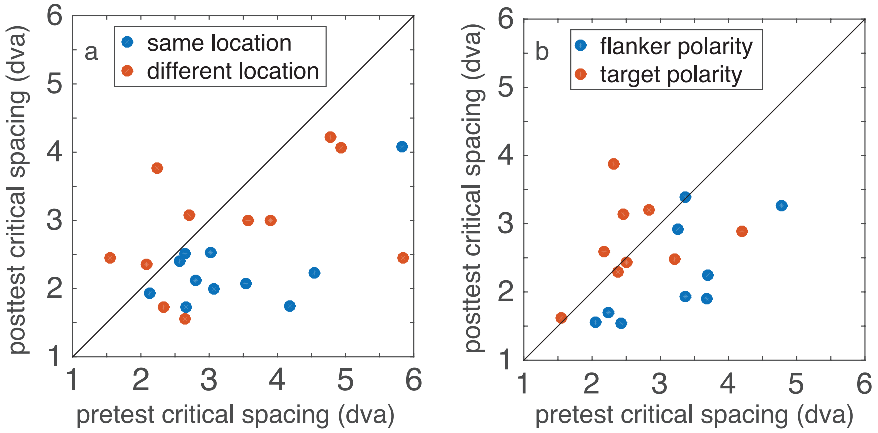

Figure 5. Scatterplot for individual subjects critical spacing during the pre- (*x*-axis) and post- (*y*-axis) tests for (a) same-location and different-location groups in Experiment 1, and (b) flanker-polarity and target-polarity groups in Experiment 2.

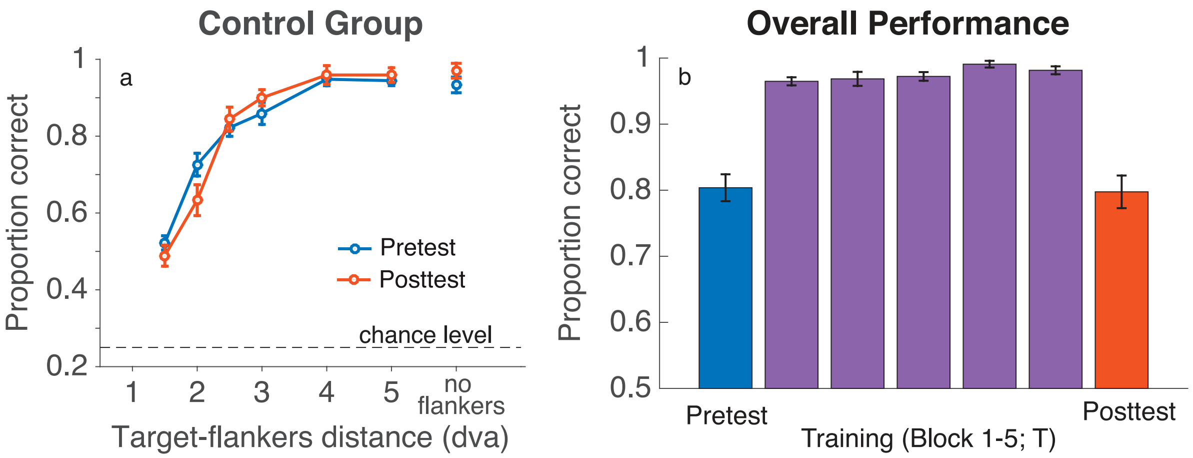

Figure 6. (a) Mean proportion correct as a function of target–flankers distance in dva for pre- and posttests in the control experiment. (b) Mean proportion correct throughout the five training blocks. Error bars correspond to ±1 *SE*.

conditions in which the target is easily segmented from the flankers will transfer to a nonsegmented crowding display, and if so, whether this learning reflects target enhancement or flankers suppression. We manipulated stimulus salience to facilitate the segmentation of the target from distractors during training by using different contrast polarity for target and flankers (e.g., if the target was white, the flankers were black and vice versa). This manipulation has been used to reduce interference in crowding (Chakravarthi & Cavanagh, 2007; Chung & Mansfield, 2009; Kooi et al., 1994; Tripathy, Cavanagh, & Bedell, 2014).

There were two groups of observers: flankers-polarity group, in which flankers were kept the same polarity between the training and the pre- and posttests, and the target-polarity group, in which the target was kept the same polarity between the training and the pre- and posttests. For both groups, the flankers and targets had matched polarity during the posttest. If observers learn to inhibit flankers based on their features then we would expect more improvement in the flankers-polarity group than the target-polarity group. Conversely, if observers learn to select the target, then we would expect more improvement in the target-polarity group than the flankers-polarity group.

Method

Observers: Eighteen New York University undergraduate male and female students participated for course credit. All reported having normal or corrected-to-normal visual acuity and normal color vision.

Stimuli and procedure: The stimuli procedure and design were the same as those in Experiment 1 except for the training phase. During training the target was white while flankers were black (or vice versa). In the flankers-polarity group, the polarity of the distractor during training was the same as during pre- and posttests. In the target-polarity group, the polarity of the target during training was the same as during pre- and posttests (Figure 1c).

Results

Critical spacing: The average adjusted R^2 of the model was 85% ($SE = 1.9\%$). Observers whose R^2 *z*-score was ≤ -3 were replaced so that each group had nine observers. Mean accuracy as a function of target spacing for pre- and posttest in each group is depicted in Figure 7. Mean critical spacing for the different groups is presented in Table 1. An ANOVA with learning (pre- vs. posttest) as within-subjects and training group as between-subjects was conducted on critical spacing. The main effect of group was not significant, $F < 1$. The main effect of learning was significant, $F(1, 16) = 5.93$, $p < 0.027$, as well as its interaction with group, $F(1, 16) = 9.03$, $p < 0.009$. One sample *t* test revealed that learning significantly reduced critical spacing in the flanker-polarity group $t(8) = 4.46$, $p < 0.002$, but not in the target-polarity group, $t(8) < 1$. Figure 4 shows the difference in critical spacing for each group. A scatterplot (Figure 5b) with the data for the individual observers shows that whereas all observers in the flanker-polarity group showed reduction of the critical spacing between the pre- and posttest, only two observers in the target-polarity group showed reduction in the critical spacing.

With the two-line fitting method, the average adjusted R^2 was 82% ($SE = 4\%$). The pattern of results is similar to that of the first model. The interaction between group and training, $F(1, 16) = 5.98$, $p < 0.0265$, emerged because the critical spacing was reduced only in the flanker-polarity group, $t(8) = 3.06$, $p = 0.007$, but not in the target-polarity group, $t < 1$.

Accuracy: A ($6 \times 2 \times 2$) three-way ANOVA was conducted with target–flankers distance (1.5, 2.0, 2.5,

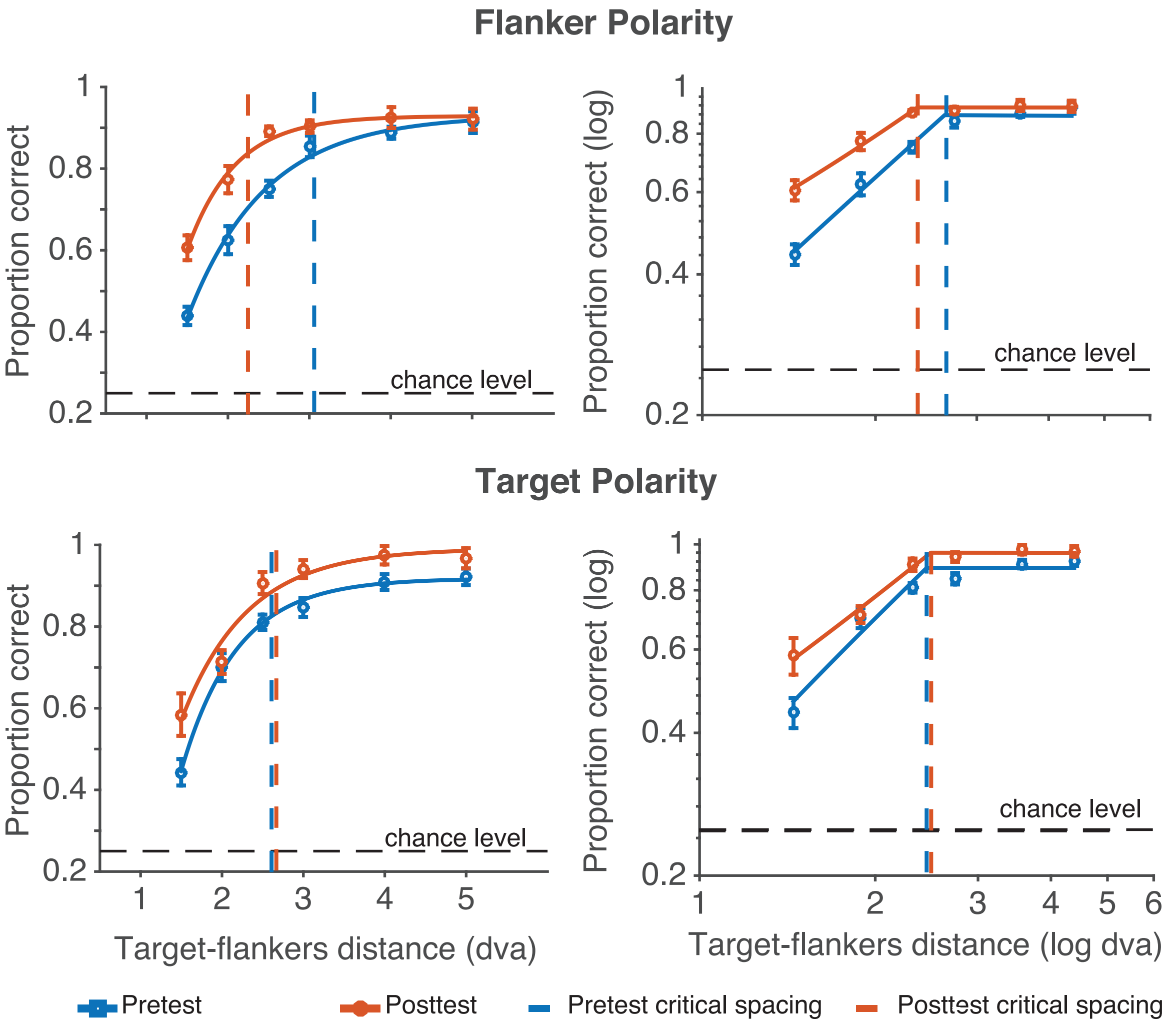

Figure 7. Mean proportion correct as a function of target–flanker distance in dva for pre- and posttests in Experiment 2 for the flankers-polarity group (top panel) and target-polarity group (bottom panel). For each group we plotted proportion correct as a function of target–flankers distance along with the exponential curve model (left panels) and two-line fitting method (right panels). Error bars correspond to ±1 *SE*. Dashed lines indicate the estimated critical spacing for each group. The two-line fitting was plotted with log–log axes. The adjusted R^2 for the fitting are 0.98, 0.96, 0.98, and 0.95 for the top-left, bottom-left, top-right, and bottom-right panels, respectively.

3.0, 4.0, and 5.0 dva), learning (pre- and posttest) as within-subjects conditions and group as between-subjects conditions. The main effects of learning as well as spacing were significant, $F(1, 16) = 20.33$, $p < 0.0001$, and $F(5, 80) = 115.44$, $p < 0.0001$, respectively. The main effect of group was not significant, $F < 1$. The three-way interaction among learning, spacing, and group, $F(5, 80) = 2.31$, $p = 0.05$, indicated that the effect of learning on the spacing effect was group-dependent. The interaction between learning and spacing was significant in the flanker-polarity group, $F(5, 40) = 5.34$, $p = 0.001$, but not in the target-polarity group, $F(5, 40) = 1.62$, $p > 0.1$. This finding indicates that learning modulated the spacing effect only in the flanker-polarity group.

Experiment 3

In Experiments 1 and 2 we show that training can rapidly reduce crowding. To test the persistence of this reduction, in Experiment 3 we conducted a follow-up test. Seven observers from the two groups that showed significant learning (four from the same-location group in Experiment 1 and three from the flanker-polarity group in Experiment 2) were retested again 8–12 months after the single training session.

Method

Observers: Seven New York University undergraduate male and female students participated for course credit.

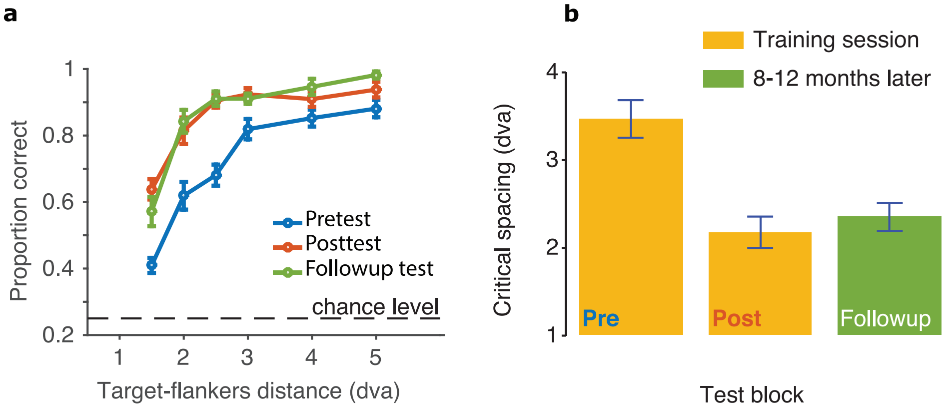

Figure 8. Results in Experiment 3. (a) Mean proportion correct as a function of target–flanker distance in dva for pre-, post-, and the follow-up tests. (b) The critical spacing for the pre-, post-, and follow-up tests. Error bars correspond to ±1 *SE*.

All reported having normal or corrected-to-normal visual acuity and normal color vision.

Stimuli and procedure: The stimuli procedure and design were the same as those in Experiment 1 except for the following changes: The experiment consisted of one test block (no training and no posttest block). During the test block there were 40 trials in each of the six target-flanker distances (240 trials overall).

Results and discussion

Critical spacing: We use the exponential curve model to calculate the critical spacing. The average adjusted R^2 of the model was 85% ($SE = 2.5\%$). Mean accuracy as a function of target spacing for pre- and posttest is depicted in Figure 8a. The critical spacing of the pre-, post-, and follow-up conditions is presented in Figure 8b. Planned comparisons revealed a significant reduction of the critical spacing in the follow-up test compared to the pretest block, $t(6) = 4.09$, $p < 0.0065$. The critical spacing in the following test was not significantly different than that in the posttest, $t < 1$. The same pattern of results was found with the two-line method.

Accuracy: A (6×3) two-way ANOVA was conducted with target–flankers distance (1.5, 2.0, 2.5, 3.0, 4.0, and 5.0 dva), and learning (pre-, post-, and follow-up tests) as within-subjects conditions. The main effects of learning and spacing were significant, $F(2, 12) = 16.24$, $p < 0.0004$, and $F(5, 30) = 53.19$, $p < 0.0001$, respectively. The interaction between spacing and learning was significant, $F(10, 60) = 3.41$, $p < 0.0015$, indicating that learning varies as a function of distance between target and flankers. Planned comparisons revealed a significant learning effect on overall accuracy between pretest and follow-up test, $t(6) = 3.94$, $p = 0.0076$, which did not significantly differ from the posttest, $t < 1$. These results show that the reduction of crowding through short training is persistent for 8–12 months. This result indicates that improvement in the initial session resulted in long-term plasticity.

General discussion

The present results demonstrate that short training can substantially alleviate crowding, causing a significant reduction of the critical spacing after only 600 training trials (Experiment 1). The improvement was higher at the trained location than at the untrained location—that is, there was some partial transfer between different locations (i.e., the left and the right hemifields). There was no learning when observers trained with an uncrowded target (control experiment), ruling out the possibilities that the results of Experiment 1 reflected either procedural learning or just target-related processing. Reduction of the critical spacing was specific to the contrast polarity of the flankers but not of the target, suggesting that learning reflects flanker-related processing (Experiment 2). The pattern of results of both experiments was consistent using two different ways to assess critical spacing, namely the exponential curve (e.g., Grubb et al., 2013; Rashal & Yeshurun, 2014; Scolari et al., 2007; Yeshurun & Rashal, 2010) and the two-line method (e.g., Chung, 2002; Chung et al., 2001; Levi et al., 2007; Pelli et al., 2004; Yeshurun & Rashal, 2010). Remarkably, the reduction of crowding persisted for 8–12 months even without additional training (Experiment 3).

Letter recognition, the mechanism underlying successful performance of the task used here, is proposed to involve two stages of perception (e.g., Pelli & Tillman, 2008; Suchow & Pelli, 2013); detecting the two lines of the T and their orientation and combining them in the correct spatial arrangement (e.g., that the horizontal line is above the vertical line). Within this theoretical framework we argue that whereas an improvement in the first stage of basic feature discrimination/detection would have resulted merely in overall improvement, the reduction of the critical spacing suggests facilitation of the second stage: feature integration. The fact that perceptual learning emerges so quickly is consistent with the finding that training induces fast improvement in the combination of features across space (Suchow & Pelli, 2013) and supports the view that crowding results from flanker interference during the process of feature integration (Pelli et al., 2004).

Previous studies have shown that grouping of flankers reduces crowding (e.g., Livne & Sagi, 2007; Saarela, Sayim, Westheimer, & Herzog, 2009). However, improvement in the present study cannot be explained by the involvement of a grouping effect in learning. First, the orientations of the two flankers were independent, which prevented grouping by shape. Second, in all test conditions contrast polarity was the same for the target and flankers, which precluded an effect of grouping by contrast polarity during tests.

One of the hallmarks of perceptual learning is its specificity to the trained locations and features (e.g., Fahle, 2004; Sowden, Rose, & Davies, 2002), which has been considered to reflect changes in early visual areas such as V1, where location and feature are represented with high resolution (for reviews, see Sagi, 2011; Shibata, Sagi, & Watanabe, 2014). However, under certain conditions learning can transfer to a different location. For example, learning transferred to a new location when observers were also trained with a different task at the transfer location (e.g., Xiao et al., 2008), when adaptation was prevented during training in a texture segmentation task (Harris, Gliksberg, & Sagi, 2012), or when observers trained with exogenous attention (Donovan, Szpiro, & Carrasco, 2015). Some of these findings have been taken to suggest that perceptual learning reflects the readout of early visual areas by higher areas related to perceptual decision (e.g., Dosher, Jeter, Liu, & Lu, 2013; Jeter et al., 2009; Xiao et al., 2008; Zhang et al., 2010). The fact that the fast learning in crowding was greater at the trained than the untrained location suggests that some aspects of this learning involve early visual areas. The fact that in Experiment 1 the learning partially transferred between the right and left hemifields suggests that learning also involved higher perceptual decision areas.

Critical spacing changes as a function of eccentricity (Levi, 2008; Pelli, & Tillman, 2008) in a ratio varying between 0.3 and 0.6 (which can be modified by various manipulations; for a review see Levi, 2008). Our pretest critical spacing is within this range (~3.3 dva at 9 dva of eccentricity). Training in the same-location group and in the flanker-polarity group reduced the critical spacing by around 32% to ~2.3 dva. Changes in the critical spacing suggest a change in spatial resolution (e.g., Pelli et al., 2004; Pelli & Tillman, 2008; Wilkinson, Wilson, & Ellemberg, 1997; Van den Berg, Roerdink, & Cornelissen, 2010). Reduction of the critical spacing, whether by exogenous attention (Grubb et al., 2013; Yeshurun & Rashal, 2010) or by training (Chung, 2007), suggests a possible change in spatial resolution (e.g., Carrasco & Barbot, 2015; Freeman & Simoncelli, 2011; Yeshurun & Rashal, 2010). These findings along with the current study place a constraint on any explanation of crowding. In particular it challenges any explanation that rely on "fixed wire length" horizontal connection between neurons in V1 (see Levi, 2008, for review). Furthermore, our finding suggests that a fundamental characteristic of any underlying neural mechanism of crowding should account for rapid yet persistent plasticity.

The results of Experiment 2 provide a unique dissociation between target and flankers training. The fact that learning was specific to the contrast polarity of the flankers but not of the target suggests that improvement was primarily driven by suppression of the flankers' signals rather than by enhancement of the target signal. Previous studies have shown that observers rely on differences in contrast polarity between the target and the flanker to separate target object from flankers to overcome crowding (Chakravarthi & Cavanagh, 2007; Chung & Mansfield, 2009; Kooi et al, 1994; Tripathy et al., 2014). Here we show that this separation relies mainly on suppression of flankers: Training with flankers and target of opposite polarity facilitated the reduction of the critical spacing of crowding, but only if the flankers had the same polarity during training and posttest. The finding that there was no improvement in the flankers-polarity group for the large target-to-flankers distances suggests that when the flankers are not interfering, training with a target with different contrast polarity no longer benefits performance. Alternatively, when observers trained with the same target polarity (target-polarity group) they showed improvement across distances, suggesting that when there is small or no flanker interference, observers still benefit from training with a target with the same polarity.

Our study is also the first to show that short training induces persistent (over a few months and even a year) learning. Several studies have shown that prolonged training induces learning that is persistent over months (Watanabe et al., 2002) and even 2–3 years (e.g., Karni & Sagi, 1993). However, with fast perceptual learning, persistence had been shown for only few weeks (Fiorentini & Berardi, 1980). Here we show that even with short training there was almost no forgetting of the learning. Retesting 8–12 months after training and without any further training showed the same critical spacing as in the posttest. Thus, fast learning in crowding reflects long-term plasticity rather than short-term sensitization.

It is important to note that except for the control experiment, in all training blocks, we varied the target–flankers distance to keep performance around ±79% correct, using a staircase. This procedure enabled us to maintain the same level of difficulty across the different training conditions, and to rule out the possibility that difficulty level (Ahissar & Hochstein 1997; Jeter et al., 2009) may underlie differences in learning among conditions.

Several studies have demonstrated that crowding is reduced by several conditions, which can be coarsely divided into two categories: (a) stimulus-driven factors, such as separating the target from the flankers by contrast polarity, depth, color, or shape (Chakravarthi & Cavanagh, 2007; Chung & Mansfield, 2009; Kooi et al., 1994; Tripathy et al., 2014), by abrupt onset (Greenwood, Sayim, & Cavanagh, 2014), by flankers grouping (e.g., Livne & Sagi, 2007; Saarela et al., 2009), by spatial configuration across the visual field (Herzog et al., 2015), and by exogenous attention (e.g., Grubb et al., 2013; Yeshurun & Rashal, 2010); and (b) conceptually driven factors, such as endogenous attention (Montaser-Kouhsari & Rajimehr, 2004) and perceptual learning (e.g., Chung, 2007; Hussain et al., 2012).

Whereas understanding stimulus-driven factors can help us design an environment that minimizes the negative effect of crowding, such as when designing an airplane cockpit, understanding conceptually driven factors can help us understand how to release crowding in situations when we have little control over the environment. The present findings can help to develop perceptual learning protocols that induce rapid learning but long-lasting reduction of crowding conditions. Our finding that learning transfers to a new target as long as the flankers remain the same suggests that an efficient protocol should focus on the characteristics of the flankers more than on those of the target. Such protocols could be implemented in the neuro-rehabilitation of developmental and age-related conditions such as amblyopia and macular degeneration.

Keywords: crowding, perceptual learning, contrast polarity

Acknowledgments

This study was supported by a National Institutes of Health R01 EY016200 grant to MC and a Fulbright fellowship to AY. We would like to thank Yimeng Hou for her help in collecting data, and Ian Donovan for his comments on a draft of this paper.

Commercial relationships: none.

Corresponding author: Amit Yashar.
Email: amityash@gmail.com.
Address: Department of Psychology, New York University, New York, NY, USA.

References

Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, *387*(6631), 401–406.

Anton-Erxleben, K., & Carrasco, M. (2013). Attentional enhancement of spatial resolution: Linking behavioural and neurophysiological evidence. *Nature Reviews Neuroscience*, *14*(3), 188–200.

Beaunieux, H., Hubert, V., Witkowski, T., Pitel, A. L., Rossi, S., Danion, J. M., & Eustache, F. (2006). Which processes are involved in cognitive procedural learning? *Memory*, *14*(5), 521–539.

Bonneh, Y. S., Sagi, D., & Polat, U. (2007). Spatial and temporal crowding in amblyopia. *Vision Research*, *47*(14), 1950–1962.

Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature*, *226*, 177–178.

Carrasco, M., & Barbot, A. (2015). How attention affects spatial resolution. *Cold Spring Harbor Symposia on Quantitative Biology*, *79*, 149–160.

Carrasco, M., Ponte, D., Rechea, C., & Sampedro, M. J. (1998). "Transient structures": The effects of practice and distractor grouping on within-dimension conjunction searches. *Perception & Psychophysics*, *60*(7), 1243–1258.

Chakravarthi, R., & Cavanagh, P. (2007). Temporal properties of the polarity advantage effect in crowding. *Journal of Vision*, *7*(2):11, 1–13, doi:10.1167/7.2.11. [PubMed] [Article]

Chung, S. T. (2002). The effect of letter spacing on reading speed in central and peripheral vision *Reading, 1270,* 1276.

Chung, S. T. (2007). Learning to identify crowded letters: Does it improve reading speed? *Vision Research*, *47*(25), 3150–3159.

Chung, S. T., Levi, D. M., & Legge, G. E. (2001). Spatial-frequency and contrast properties of crowding. *Vision Research*, *41*(14), 1833–1850.

Chung, S. T., Li, R. W., & Levi, D. M. (2012). Learning to identify near-acuity letters, either with or without flankers, results in improved letter size and spacing limits in adults with amblyopia. *PLoS ONE*, *7*(4), e35829.

Chung, S. T., & Mansfield, J. S. (2009). Contrast polarity differences reduce crowding but do not benefit reading performance in peripheral vision. *Vision Research*, *49*(23), 2782–2789.

Cohen, N. J., & Squire, L. R. (1980). Preserved learning and retention of pattern analysing skill in amnesia: Dissociation of knowing how and knowing that. *Science*, *210*, 207–210.

Donovan, I., Szpiro, S., & Carrasco, M. (2015). Exogenous attention facilitates location transfer of perceptual learning. *Journal of Vision*, *15*(10):11, 1–16, doi:10.1167/15.10.11. [PubMed] [Article]

Dosher, B. A., Jeter, P., Liu, J., & Lu, Z. L. (2013). An integrated reweighting theory of perceptual learning. *Proceedings of the National Academy of Sciences, USA*, *110*(33), 13678–13683.

Dosher, B. A., & Lu, Z. L. (1999). Mechanisms of perceptual learning. *Vision Research*, *39*(19), 3197–3221.

Fahle, M. (2004). Perceptual learning: A case for early selection. *Journal of Vision*, *4*(10):4, 879–890, doi:10.1167/4.10.4. [PubMed] [Article]

Fahle, M., & Poggio, T. (2002). *Perceptual learning*. Cambridge, MA: MIT Press.

Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, *287*(5777), 43–44.

Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research*, *21*(7), 1149–1158.

Frank, S. M., Reavis, E. A., Tse, P. U., & Greenlee, M. W. (2014). Neural mechanisms of feature conjunction learning: enduring changes in occipital cortex after a week of training. *Human Brain Mapping*, *35*(4), 1201–1211.

Freeman, J., & Simoncelli, E. P. (2011). Metamers of the ventral stream. *Nature Neuroscience*, *14*(9), 1195–1201.

Greenwood, J. A., Bex, P. J., & Dakin, S. C. (2010). Crowding changes appearance. *Current Biology*, *20*(6), 496–501.

Greenwood, J. A., Sayim, B., & Cavanagh, P. (2014). Crowding is reduced by onset transients in the target object (but not in the flankers). *Journal of Vision*, *14*(6):2, 1–21, doi:10.1167/14.6.2. [PubMed] [Article]

Grubb, M. A., Behrmann, M., Egan, R., Minshew, N. J., Heeger, D. J., & Carrasco, M. (2013). Exogenous spatial attention: Evidence for intact functioning in adults with autism spectrum disorder. *Journal of Vision*, *13*(14):9, 1–13, doi:10.1167/13.14.9. [PubMed] [Article]

Harris, H., Gliksberg, M., & Sagi, D. (2012). Generalized perceptual learning in the absence of sensory adaptation. *Current Biology*, *22*(19), 1813–1817.

Husk, J. S., Bennett, P. J., & Sekuler, A. B. (2007). Inverting houses and textures: Investigating the characteristics of learned inversion effects. *Vision Research*, *47*(27), 3350–3359.

Hussain, Z., Webb, B. S., Astle, A. T., & McGraw, P. V. (2012). Perceptual learning reduces crowding in amblyopia and in the normal periphery. *Journal of Neuroscience*, *32*(2), 474–480.

Herzog, M. H., Sayim, B., Chicherov, B., & Manassi, M. (2015). Crowding, grouping, and object recognition: A matter of appearance. *Journal of Vision*, *15*(6):5, 1–18, doi:10.1167/15.6.5. [PubMed] [Article].

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences*, *88*(11), 4966–4970.

Karni, A., & Sagi, D. (1993). The time course of learning a visual skill. *Nature*, *365*(6443), 250–252.

Kooi, F. L., Toet, A., Tripathy, S. P., & Levi, D. M. (1994). The effect of similarity and duration on spatial interaction in peripheral vision. *Spatial Vision*, *8*(2), 255–279.

Jeter, P. E., Dosher, B. A., Petrov, A., & Lu, Z. L. (2009). Task precision at transfer determines specificity of perceptual learning. *Journal of Vision*, *9*(3):1, 1–13, doi:10.1167/9.3.1. [PubMed] [Article]

Levi, D. M. (2008). Crowding—An essential bottleneck for object recognition: A mini-review. *Vision Research*, *48*(5), 635–654.

Levi, D. M., Song, S., & Pelli, D. G., (2007). Amblyopic reading is crowded. *Journal of Vision*, *7*(2):21, 1–17, doi:10.1167/7.2.21. [PubMed] [Article]

Levitt, H. C. C. H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America*, *49*(2B), 467–477.

Livne, T., & Sagi, D. (2007). Configuration influence on crowding. *Journal of Vision*, *7*(2):4, 1–12, doi:10.1167/7.2.4. [PubMed] [Article]

Lu, Z. L., Chu, W., Dosher, B. A., & Lee, S. (2005). Independent perceptual learning in monocular and binocular motion systems. *Proceedings of the National Academy of Sciences, USA, 102*(15), 5624–5629.

Montaser-Kouhsari, L., & Rajimehr, R. (2005). Subliminal attentional modulation in crowding condition. *Vision Research*, *45*(7), 839–844.

Mukai, I., Kim, D., Fukunaga, M., Japee, S., Marrett, S., & Ungerleider, L. G. (2007). Activations in visual and attention-related areas predict and correlate with the degree of perceptual learning. *Journal of Neuroscience*, *27*(42), 11401–11411.

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience*, *4*(7), 739–744.

Pelli, D. G., Burns, C. W., Farell, B., & Moore-Page, D. C. (2006). Feature detection and letter identification. *Vision Research*, *46*(28), 4646–4674.

Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking: Distinguishing feature integration from detection. *Journal of Vision*, *4*(12):12, 1136–1169, doi:10.1167/4.12.12. [PubMed] [Article]

Pelli, D. G., & Tillman, K. A. (2008). The uncrowded window of object recognition. *Nature Neuroscience*, *11*(10), 1129–1135.

Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science*, *256*(5059), 1018–1021.

Polat, U. (2008). Restoration of underdeveloped cortical functions: Evidence from treatment of adult amblyopia. *Restorative Neurology & Neuroscience*, *26*(4), 413–424.

Rashal, E., & Yeshurun, Y. (2014). Contrast dissimilarity effects on crowding are not simply another case of target saliency. *Journal of Vision*, *14*(6):9, 1–12, doi:10.1167/14.6.9. [PubMed] [Article]

Saarela, T. P., Sayim, B., Westheimer, G., & Herzog, M. H. (2009). Global stimulus configuration modulates crowding. *Journal of Vision*, *9*(2):5, 1–11, doi:10.1167/9.2.5. [PubMed] [Article]

Sagi, D. (2011). Perceptual learning in vision research. *Vision Research*, *51*(13), 1552–1566.

Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology*, *483*(3), 797–810.

Scolari, M., Kohnen, A., Barton, B., & Awh, E. (2007). Spatial attention, preview, and popout: Which factors influence critical spacing in crowded displays? *Journal of Vision*, *7*(2):7, 1–23, doi:10.1167/7.2.7. [PubMed] [Article]

Shibata, K., Sagi, D., & Watanabe, T. (2014). Two-stage model in perceptual learning: Toward a unified theory. *Annals of the New York Academy of Sciences*, *1316*(1), 18–28.

Sowden, P. T., Rose, D., & Davies, I. R. (2002). Perceptual learning of luminance contrast detection: Specific for spatial frequency and retinal location but not orientation. *Vision Research*, *42*(10), 1249–1258.

Strasburger, H., Rentschler, I., & Jüttner, M. (2011). Peripheral vision and pattern recognition: A review. *Journal of Vision*, *11*(5):13, 1–82, doi:10.1167/11.5.13. [PubMed] [Article]

Suchow, J. W., & Pelli, D. G. (2013). Learning to detect and combine the features of an object. *Proceedings of the National Academy of Sciences*, *110*(2), 785–790.

Szpiro, S. F., Spering, M., & Carrasco, M. (2014). Perceptual learning modifies untrained pursuit eye movements. *Journal of Vision*, *14*(8):8, 1–13, doi:10.1167/14.8.8. [PubMed] [Article]

Szpiro, S. F., Wright, B. A., & Carrasco, M. (2014). Learning one task by interleaving practice with another task. *Vision Research*, *101*, 118–124.

Tripathy, S. P., Cavanagh, P., & Bedell, H. E. (2014). Large crowding zones in peripheral vision for briefly presented stimuli. *Journal of Vision*, *14*(6):11, 1–11, doi:10.1167/14.6.11. [PubMed] [Article]

Van den Berg, R., Roerdink, J. B., & Cornelissen, F. W. (2010). A neurophysiologically plausible population code model for feature integration explains visual crowding. *PLoS Computational Biology*, *6*(1), e1000646.

Wang, R., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2014). Vernier perceptual learning transfers to completely untrained retinal locations after double training: A "piggybacking" effect. *Journal of Vision*, *14*(13):12, 1–10, doi:10.1167/14.13.12. [PubMed] [Article]

Wang, X., Zhou, Y., & Liu, Z. (2013). Transfer in motion perceptual learning depends on the difficulty of the training task. *Journal of Vision*, *13*(7):5, 1–9, doi:10.1167/13.7.5. [PubMed] [Article]

Watanabe, T., Náñez, J. E., Koyama, S., Mukai, I., Liederman, J., & Sasaki, Y. (2002). Greater plasticity in lower-level than higher-level visual motion processing in a passive perceptual learning task. *Nature Neuroscience*, *5*(10), 1003–1009.

Watanabe, T., Náñez, J. E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature*, *413*(6858), 844–848.

Whitney, D., & Levi, D. M. (2011). Visual crowding: A fundamental limit on conscious perception and object recognition. *Trends in Cognitive Sciences*, *15*(4), 160–168.

Wilkinson, F., Wilson, H. R., & Ellemberg, D. (1997). Lateral interactions in peripherally viewed texture arrays. *Journal of the Optical Society of America A*, *14*(9), 2057–2068.

Xiao, L. Q., Zhang, J. Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology*, *18*(24), 1922–1926.

Yeshurun, Y., & Rashal, E. (2010). Precueing attention to the target location diminishes crowding and reduces the critical distance. *Journal of Vision*, *10*(10):16, 1–12, doi:10.1167/10.10.16. [PubMed] [Article]

Zhang, J. Y., Zhang, G. L., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *Journal of Neuroscience*, *30*(37), 12323–12328.