

Original Articles

Rapid and long-lasting learning of feature binding

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ABSTRACT

How are features integrated (bound) into objects and how can this process be facilitated? Here we investigated the role of rapid perceptual learning in feature binding and its long-lasting effects. By isolating the contributions of individual features from their conjunctions between training and test displays, we demonstrate for the first time that training can rapidly and substantially improve feature binding. Observers trained on a conjunction search task consisting of a rapid display with one target-conjunction, then tested with a new target-conjunction. Features were the same between training and test displays. Learning transferred to the new target when its conjunction was presented as a distractor, but not when only its component features were presented in different conjunction distractors during training. Training improvement lasted for up to 16 months, but, in all conditions, it was specific to the trained target. Our findings suggest that with short training observers' ability to bind two specific features into an object is improved, and that this learning effect can last for over a year. Moreover, our findings show that while the short-term learning effect reflects activation of presented items and their binding, long-term consolidation is task specific.

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1. Introduction

A successful interaction with the visual environment requires integrated representation of objects' features. For example, when driving a car it is important to efficiently recognize that a circle shaped light is red and belongs to the stoplight. Numerous studies have shown, however, that in some situations observers tend to be inefficient in correctly integrating or binding features together. For example, observers' detection of a target defined by a conjunction of orientation and color (conjunction search; e.g., Carrasco, Evert, Chang, & Katz, 1995; Treisman & Gelade, 1980) or orientation and spatial frequency (Carrasco & McElree, 2001; Giordano, McElree, & Carrasco, 2009), is substantially slower and less accurate than detection of a target defined by a single feature. These findings and the existence of 'illusory conjunctions' (e.g., Robertson, 2003 for review) have been taken to suggest that feature integration relies on the allocation of processing resources in space, i.e., spatial attention (e.g., Prinzmetal, Presti, & Posner, 1986; Treisman & Gelade, 1980; Wolfe, 2012) (but see Di Lollo (2012)).

However, it is still unclear whether cognitive capacities beside attention play a role in feature binding. Although it has been

suggested that experience might affect feature binding (e.g., Robertson, 2003), thus far there is no direct evidence for this idea. In visual perception, experienced-based learning and long-term plasticity have been demonstrated in numerous perceptual tasks, a phenomenon known as *perceptual learning* (reviewed by Sagi (2011)). Studies of perceptual learning typically focus on the perception of isolated features, such as orientation (e.g. Ahissar & Hochstein, 1997; Jeter, Dosher, Petrov, & Lu, 2009; Donovan, Szpiro, & Carrasco, 2015; Szpiro & Carrasco, 2015), motion (e.g., Ball & Sekuler, 1982; Szpiro, Sperling, & Carrasco, 2014; Watanabe, Náñez, & Sasaki, 2001), and spatial frequency (e.g., Fiorentini & Berardi, 1981). The improvement is usually specific to the trained features and locations and considered to reflect changes in early visual representation of features (e.g. Adab & Vogels, 2011; Crist, Li, & Gilbert, 2001). Some studies showed that training can speed conjunction search (e.g. Carrasco, Ponte, Rechea, & Sampredo, 1998; Frank, Reavis, Tse, & Greenlee, 2014; Su et al., 2014; Walsh, Ashbridge, & Cowey, 1998), which requires not only detecting and discriminating features, but also binding them together. But it is unknown whether the improvements observed in feature-conjunction search reflect improvement in feature representation (*feature-learning*), feature binding (*binding-learning*) or both. If improvement reflects feature learning alone then learning should be specific just to the trained features, if improvement reflects binding learning then learning may be specific to the trained bindings as well.

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To address this question we had observers training during a single session with a brief display of a color-orientation conjunction search. In Experiment 1 we tested whether learning is limited to the specific conjunctions of the specific features presented in the training display (binding learning, e.g., [Robertson, 2003](#)), or (b) can be generalized to non-presented conjunctions of the same features (feature learning; e.g. [Adab & Vogels, 2011](#); [Crist et al., 2001](#)). In Experiment 2 we tested whether learning occurs for a conjunction stimulus that needs to be rejected (distractor suppression; e.g., [Kristjánsson, Wang, & Nakayama, 2002](#)). Finally, we tested whether short training suffices to consolidate the learned information for extended periods by retesting observers after several (5–16) months.

2. Experiment 1

In all conditions the same four features defined all search items: two orientations (50° or 80°) and two colors (red or green). Target and distractors were defined by a particular conjunction of orientation and color. For example, when the target was a 50° tilted red line the distractors were 50° tilted green lines and 80° tilted red lines ([Fig. 1A](#)). Following six consecutive blocks with the same target, observers were tested with a new target that had both color and orientation swapped—i.e., when the training target was a 50° tilted red line the test target was an 80° tilted green line.

There were two training groups: *No-exposure* group: observers were trained with targets and distractors that were different from the subsequent test targets. *Exposure* group: unbeknownst to the observers, one or two distractors during training were the same items as the future test target. Thus, the training displays for the two groups shared >91% of the items ([Fig. 1B](#)). Regarding feature learning, given that the same features were presented during train-

ing and test for both groups, we hypothesize that feature learning will result in a complete transfer in both groups. Regarding binding-learning, given that it is necessary to bind distractors' features before they can be rejected, we hypothesize that binding learning will show more transfer when the test target was presented as a distractor during training (Exposure group) than when the test target was a new conjunction (No-exposure).

2.1. Method

2.1.1. Observers

Twenty-seven New York University undergraduate students participated for course credit (13 females, age ranged 18–25 years old). The number of observers in each of the two groups was preset to 12 (three observers who performed at chance level during training were replaced). All observers were naïve as to the purposes of the study and all reported having normal or corrected-to-normal visual acuity and normal color vision.

2.1.2. Apparatus

Observers were tested individually in a dimly lit room. An Intel Core 2 Duo computer connected to a 22" CRT monitor (iiyama Vision Master Pro 514, with 1280 × 960 resolution and 85 Hz refresh rate). Stimuli were programmed in E-prime ([Schneider, Eschman, & Zuccolotto, 2002](#)). Responses were collected via the computer keyboard. A chin-rest set the 50-cm viewing distance.

2.1.3. Stimuli and procedure

Sample stimulus displays are presented in [Fig. 1A](#). Each trial began with the presentation of the fixation display (500 ms), which was a gray cross sign (+) (0.16° × 0.16° of visual angle) in the center of a black screen, followed by a 117-ms presentation of the search stimulus, which consisted of the fixation cross along with

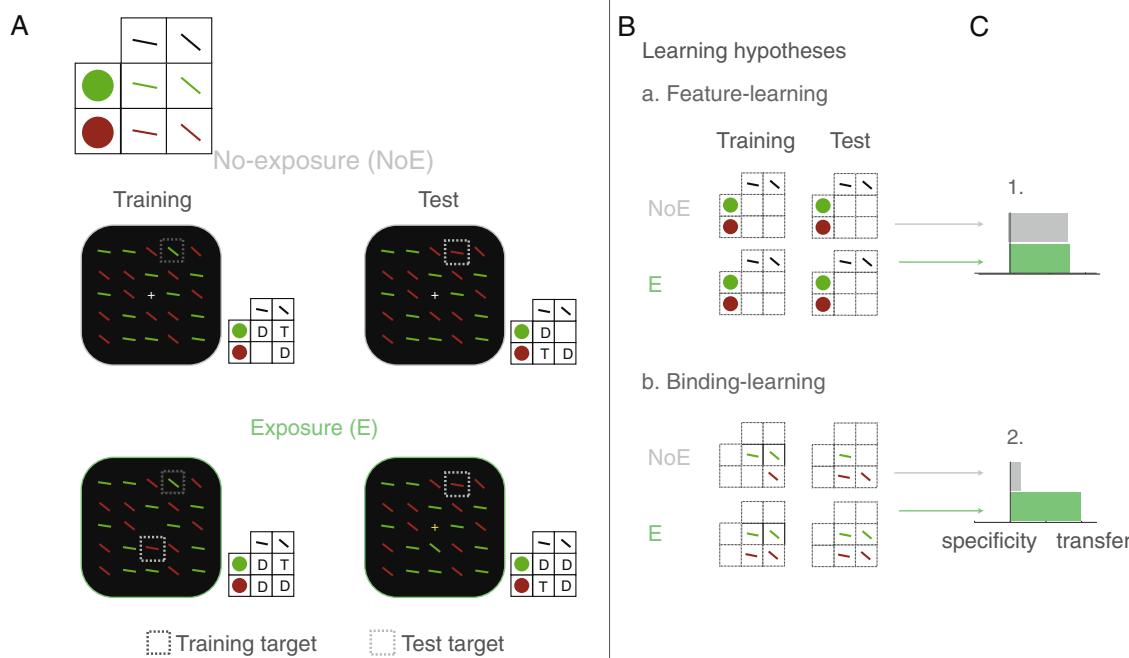


Fig. 1. Illustration of the rationale of Experiment 1, along with diagrams that represents the information that is coded in each display. (A) Sample stimulus of the training displays in the No-exposure and Exposure groups. In this example, the target (indicated by the dashed dark square) was a 50° tilted green line during training and an 80° tilted red line during test. In the Exposure group the test target was displayed during training (indicated by the solid light square). The four possible target combinations (2 colors × 2 tilts) were counterbalanced across observers. (B) A description of the two learning hypotheses. We hypothesized that training improves either (a) feature-learning (e.g., learning to identify the features i.e. a 50° tilt, an 80° tilt, a red color) or (b) binding-learning (e.g. learning the conjunction between an 80° tilt and the red color). (C) Predicted transfers between training and test for each of the training conditions. According to the (a) feature-learning, and the (b) binding-learning, learning would transfer (a) in both conditions, (b) only in the Exposure condition, respectively.

24 tilted line segments (0.38° in length). Each line appeared in one of the cells of a 5×5 matrix (except for the center cell, in which the fixation cross was presented). Each line was centered in its cell ($1^\circ \times 1^\circ$) with a random jitter of $\pm 0.01^\circ$. The lines were oriented either 80° or 50° counterclockwise from vertical and were colored either red (CIE coordinates $0.63/0.34$, 18.75 cd/m^2) or green (CIE coordinates $0.28/0.593$, 18.44 cd/m^2). Observers had to detect the presence of a target – a line defined by a specific color and orientation – among 24 items. In the No-exposure group there were two types of distractors, each type shared one feature with the target (i.e., either the same color with a different orientation or vice versa). The Exposure group included one (in target present trials) or two (in target absent trials) distractors with both a different color and a different orientation from the target (thus exposing the color-orientation conjunction of the subsequent test target). Target and distractors locations were randomly distributed in the matrix, and the specific target and distractors color and orientation conjunctions were counterbalanced across observers.

Observers were asked to report whether the target was present or absent by pressing one of two designated keyboard keys, and instructed to respond as accurately as possible without speed stress. Observers were instructed to maintain fixation throughout each trial; they had no time to make eye movements while the conjunction display was presented. A 500-ms feedback tone followed incorrect responses. There was a 500-ms inter-trial interval.

2.1.4. Design

Observers participated in one-hour experimental session that consisted of six training blocks of 120 trials each (720 trials in total), followed by one transfer test block of 120 trials. During the training blocks each observer was asked to detect a particular color and orientation conjunction and then was tested in detecting a different color and orientation conjunction during the transfer test block. The target on the test block consisted of the alternative color and the alternative orientation of the trained target (e.g., when the trained target was a 50° green line the test target was an 80° red line). Thus, in the No-exposure group the test target conjunction had never been presented during training, whereas in the Exposure group the test target conjunction had been presented during training as either one (in target present trials) or two (in target absent trials) of the 24 search items (Fig. 1B).

To familiarize observers with the procedure, each session began with 30 practice trials with different conjunctions than those used in the experimental session; namely, a 100° tilted blue target amidst 100° tilted yellow and 10° tilted blue distractors. To familiarize observers with the target, 10 example trials with a long-display duration (1 s) were presented both before the training (pre-training examples) and before the test (pre-test examples) blocks. Every 30 trials there was a short break during which observers were reminded of the target by presenting the target on the screen throughout the break.

2.1.5. Analysis

Sensitivity (d') and criterion (C) were calculated for each training and test block. To assess learning and transfer of learning separately we conducted two Analysis of Variance (ANOVA) with d' , C and reaction time (RT) as dependent variables. **Training:** To compare learning between the groups an ANOVA was conducted with training (the six training blocks, within-subjects) and training group (No-exposure vs. Exposure, between-subjects). **Transfer:** To compare transfer an ANOVA was conducted with transfer of learning (last training block vs. transfer-test block, within-subjects) and training group (between-subjects). Moreover, transfer of learning was assessed individually by calculating a variation on a commonly used transfer index (e.g., Ahissar & Hochstein,

1997; Hung & Seitz, 2014; Jeter et al., 2009; Lu, Chu, Dosher, & Lee, 2005; Zhang et al., 2010).

$$T = 1 - \frac{(d_6 - d_7)}{(d_6 - d_1)} \quad (1)$$

The values d_1 and d_6 denote the sensitivity level for the first and last blocks of the training, respectively. The value d_7 is the sensitivity for the transfer task block. This measure estimates the portion of the initial learning that is transferred. A T of 1 indicates complete transfer; when the d' of the transfer test block is equal to the final block of the training. A T of 0 indicates full specificity; when the transfer test block has the same sensitivity as the first block of training. A $T < 0$ indicates super specificity, in which d' of the transfer test block is smaller than the first training block, which can be found in cases where learning reflects inhibition of distractor.

2.2. Results

High accuracy rates for both groups during the 10 long-duration example trials before training and test (Table 1) indicate that observers had ample pre-knowledge of the test-target in both groups.

To ensure that performance was comparable for the different tested colors and orientations, we conducted an ANOVA with specific target and distractor conjunctions as a between subject factor. For learning, there was no main effect of specific conjunction nor did it interact with learning or group, all $Fs < 1$. For transfer, there was no main effect of specific conjunction nor did it interact with learning and group, all $Fs < 1$.

2.2.1. Sensitivity

Fig. 3 shows that training improved performance significantly, $F(5,110) = 24.19$, $p < 0.001$, $\eta^2 = 0.52$. There was neither a main effect of group nor a group by training interaction, both $F < 1$, indicating that learning was similar in both groups. There was a main effect of transfer, $F(1,22) = 4.97$, $p = 0.036$, $\eta^2 = 0.18$, which interacted with group, $F(1,22) = 4.55$, $p = 0.044$, $\eta^2 = 0.17$. A paired t -test revealed a significant transfer cost in the No-exposure group $t(11) = 3.42$, $p = 0.006$, $r^2 = 0.51$, but not in the Exposure group, $t(11) < 1$. These findings show that training group condition did not affect learning but rather the transfer of learning.

2.2.2. Criterion

During training, neither the main effects of training and group nor their interaction were significant, all $ps > 0.20$ (Fig. 3). The main effect of transfer-test block was significant, $F(1,22) = 41.21$, $p < 0.001$, $\eta^2 = 0.65$, but neither the main effect of group nor their interaction was significant, $F < 1$. The transfer-block effect on criterion was significant for both groups, $F(1,11) = 31.22$, $p < 0.002$, $\eta^2 = 0.73$, and $F(1,11) = 16.42$, $p = 0.002$, $\eta^2 = 0.59$. The possible effect of criterion on observed changes in d' was ruled out by a non-significant correlation between d' and criterion, $r(23) = 0.17$, $p > 0.40$.

2.2.3. RT

Training reduced RTs in both groups, $F(5,110) = 14.59$, $p < 0.001$, $\eta^2 = 0.40$. The main effect of group and the training by group interaction were both not significant, both $Fs < 1$, indicating that the accuracy results cannot be explained by speed-accuracy tradeoffs for either group (Fig. 3).

2.2.4. Transfer index

One sample t -test compared to 0 (complete specificity) revealed significant transfer ($T > 0$) in the Exposure group, $t(11) = 2.03$, $p = 0.036$, $r^2 = 0.272$, but not in the No-exposure group, $t(11)$

Table 1

Mean proportion correct for the initial ten long duration example trials with the Training stimulus and the initial ten long duration example trials with the Test stimulus for the No-exposure and Exposure groups (Experiment 1), the Color and Orientation groups (Experiment 2) and the No-exposure and Exposure (Exposure Color and Orientation) groups (Experiment 3). In all conditions performance was high, indicating that observer had the same knowledge about the training and the test target. Standard errors are in parenthesis.

	Experiment 1		Experiment 2		Experiment 3	
	No-exposure	Exposure	Color	Orientation	Exposure	No-exposure
Training stimulus	82% (4%)	83% (4%)	80% (4%)	83% (5%)	86% (3%)	92% (5%)
Test stimulus	82% (6%)	82% (6%)	83% (5%)	78% (5%)	88% (6%)	93% (3%)

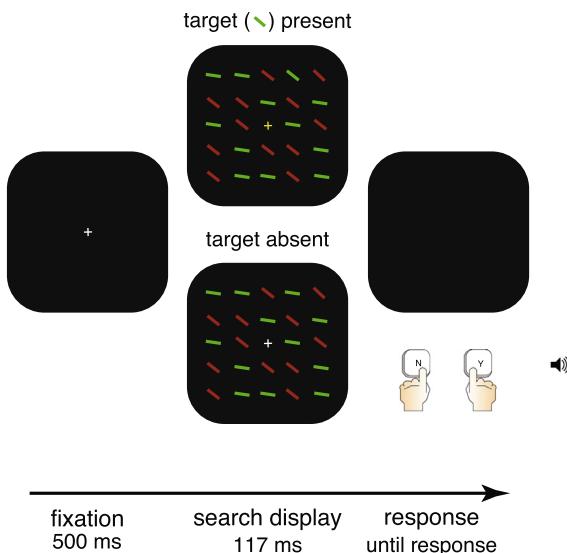


Fig. 2. An example of the sequence of events within a trial. Observers had to report whether the target, i.e. a 50° tilted counter clockwise from vertical green (light gray in a black & white print) line, was present or absent.

= 1.23, $p = 0.12$ (Fig. 4A). This finding is in line with the binding-learning hypothesis (Fig. 4B).

2.3. Discussion

Both groups showed substantial improvements after a ~45 min single session of training. Learning transferred to the test target in the Exposure group but not in the No-exposure group, even though the change in target between training and test blocks was the same for both groups. That is, learning transferred only when observers were exposed to the test-target conjunction as one or two of the distractors during training. A plot of the transfer index (Fig. 4) for each group shows that the data support the hypothesis that observers learn the binding of features (binding-learning) rather than just features identification/discrimination (feature-learning). This interaction cannot be explained by differences in observers' pre-knowledge of the target conjunction (Table 1), change in criterion or speed-accuracy trade-offs (Fig. 3).

Although the main effect of group was not significant during training, the overall performance of the No-exposure group was slightly higher than the Exposure group. This may result from the lower number of different conjunctions in the No-exposure group (three) than in the Exposure group (four). We address this issue in Experiment 2.

3. Experiment 2

In Experiment 1 we showed that exposure to the future test-target during training induces more transfer of learning than the

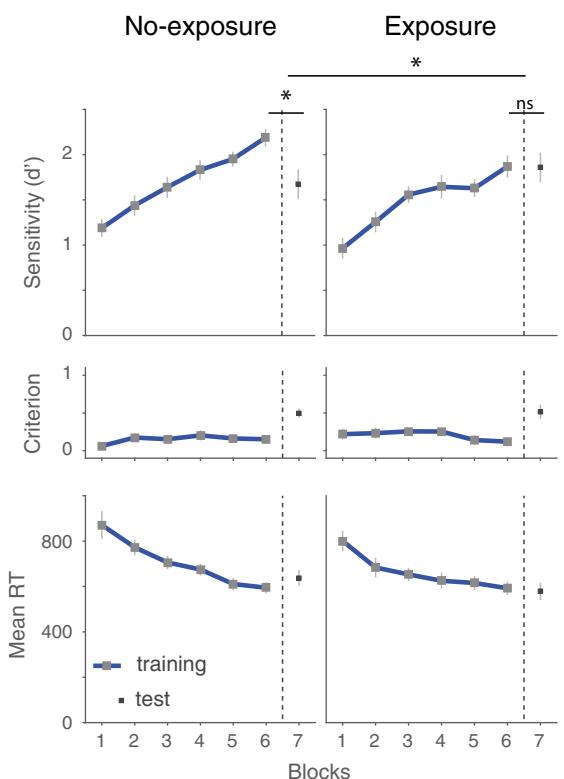


Fig. 3. Mean sensitivity (d') criterion and reaction time (RT) as a function of training (blocks 1–6) and transfer test (block 7) in the No-exposure and Exposure groups in Experiment 1. Error bars are within-subject standard errors (Morey, 2008). * $p < 0.05$.

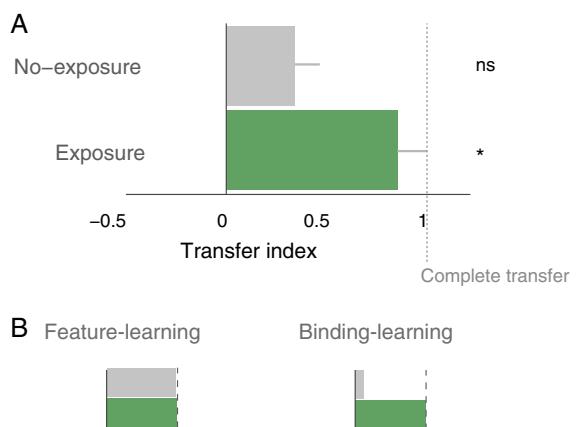


Fig. 4. (A) Mean transfer index for the No-exposure and Exposure groups in Experiment 1. Complete transfer is indicated by $T = 1$ and complete specificity by $T = 0$. Error bars are within-subject standard errors (Morey, 2008). (B) The predicted results according to the two hypotheses: (a) feature learning, (b) binding learning.

No-exposure condition. However, in that experiment the future test-target was only one or two out of 24 distractors. Thus it is possible that observers did not have to ignore and suppress the future test item. In Experiment 2 we tested whether observers learn the conjunction of an item that they have to ignore by presenting the future test-target conjunction as half (12 items) of the training distractors. If learning during training involves the inhibition of distractors' features then learning will not transfer to a target containing these features. In fact, it could even result in a performance level lower than baseline (first training block). In addition, in Experiment 1 the Exposure group contained more conjunctions combinations (four combinations) than the No-exposure group (three combination). To rule out the possibility that this difference mediates the transfer effect, in both conditions of Experiment 2 we used the same number (three) of conjunction combinations (as in the No-exposure group). Were the specificity observed in the No-exposure group of Experiment 1 due to the number of conjunction combinations, then we would expect to find a similar specificity in all conditions of Experiment 2. Two training groups were tested: *Color group*: the target swapped its color between training and test. *Orientation group*: the target swapped its orientation between training and test (Fig. 5A). In both groups the test-target was presented as a half of the distractors during training. (a) If observers learned to integrate presented features (Binding-learning, Fig. 5B) then we would expect full transfer in both groups. However, (b) if observers learned to suppress the features of a recurring distractor (Distractor suppression, Fig. 5B) then we would observe only a partial or no transfer of learning to the test block — and maybe even worse performance than the baseline (first training block).

3.1. Method

3.1.1. Observers

Twenty-eight New York University undergraduate students (20 females, age ranged 19–21 years old) participated in the experiment for course credit. All observers were naïve to the purposes of the study. All reported having normal or corrected-to-normal visual acuity and normal color vision. There were 12 observers in

each of two groups (four observers who performed at chance level during training were replaced).

3.1.2. Stimuli, procedure and design

Task, design and stimulus were the same as in Experiment 1, except that the test-target in the color group and the Orientation group swapped either its color or orientation respectively, such that a training distractor became the test-target and vice versa (Fig. 5A).

3.2. Results

As indicated by the high performance in the example trials (pre-test and pre-training) all observers had ample pre-knowledge of training-target and test-target (Table 1).

3.2.1. Sensitivity

Training significantly improved performance, $F(5, 110) = 19.34$, $p < 0.0001$, $\eta^2 = 0.467$ (Fig. 6). As expected, there was neither a main effect of group nor a group by training interaction, both $ps > 0.1$, suggesting that training effects were similar in both groups. Neither a main effect of transfer-test on performance nor a significant group by transfer-test interaction emerged, all $Fs < 1$.

3.2.2. Criterion

The main effect of training on criterion was significant, $F(5, 110) = 3.44$, $p < 0.006$, $\eta^2 = 0.135$ (Fig. 6). Neither a main effect of group nor the group by training interaction was significant, both $Fs < 1.35$. In the transfer-test block, the main effect of group was marginally significant, $F(1, 22) = 4.25$, $p = 0.0513$, $\eta^2 = 0.16$. The main effect of transfer-test block was significant, $F(1, 22) = 5.74$, $p = 0.025$, $\eta^2 = 0.20$, as well as the group by transfer-test interaction, $F(1, 22) = 5.25$, $p = 0.032$, $\eta^2 = 0.19$. Paired t -tests showed that transfer-test effect on criterion was significant in the Orientation group, $t(11) = 2.51$, $p = 0.0287$, $r^2 = 0.36$, but not in the Color group, $t(11) = 1.11$, $p = 0.29$ (Fig. 7). These results suggest that observers adopted a more conservative criterion during training than during the transfer block in the Orientation group but not in the Color group.

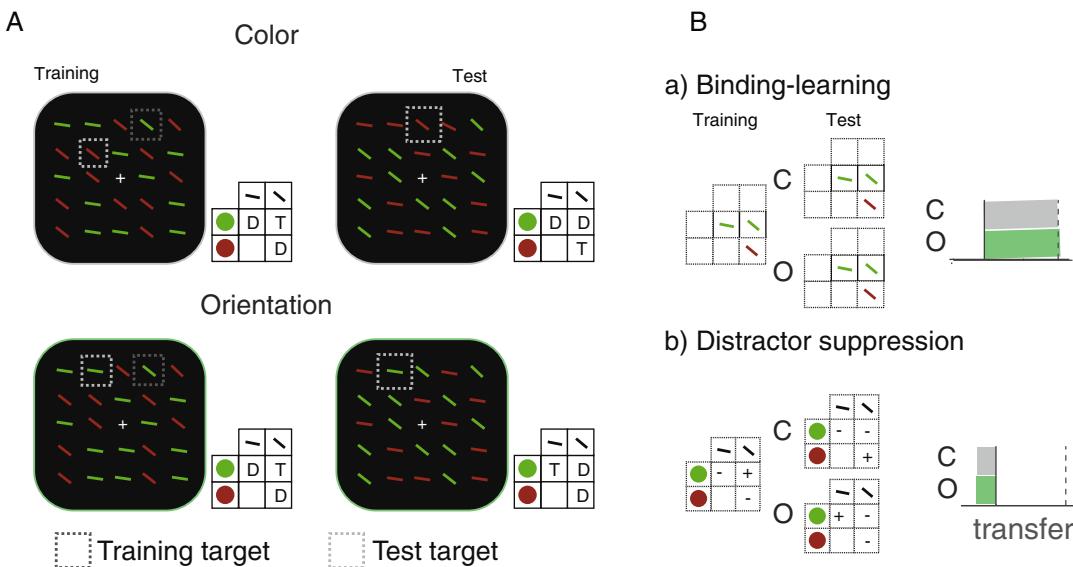


Fig. 5. Sample stimulus, hypothesis and predictions in Experiment 2. (A) Training and test search displays in the Color and Orientation groups. In this example the target was a 50° green line during training and a 50° tilted red (dark gray in a black & white print) line during the test in the Color group and 80° tilted green line during the test in the Orientation group. As in Experiment 1, the four possible target combinations (2 × 2 colors and tilts) were counterbalanced across observers. In both groups the test target was displayed during training (indicated by the dashed light square). (B) Predicted results base on the two learning hypotheses according to which improvement reflects learning of: (a) feature integration of search items (binding-learning), (b) distractor features suppression (distractor suppression).

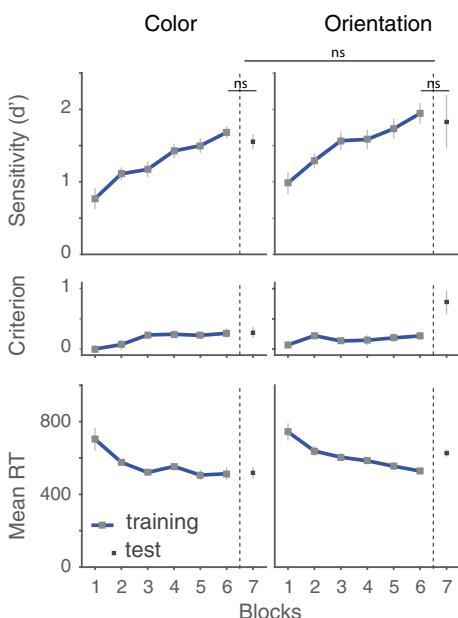


Fig. 6. Mean sensitivity (d') criterion and reaction time (RT) as a function of training (blocks 1–6) and transfer test (block 7) for the Color and the Orientation group in Experiment 2. Error bars are within-subjects standard errors (Morey, 2008).

3.2.3. RT

An ANOVA revealed that training reduced RTs, $F(5, 110) = 13.70$, $p < 0.0001$, $\eta^2 = 0.38$. Neither the main effect of group nor its interaction with training was significant, both $Fs < 1$. The main effect of transfer-test was significant, $F(1, 20) = 7.65$, $p = 0.011$, $\eta^2 = 0.25$, but the main effect of group was not, $F(1, 20) = 1.75$, $p > 0.19$. The group by transfer-test interaction was significant, $F(1, 20) = 6.33$, $p = 0.0197$, $\eta^2 = 0.23$. Paired comparisons of specificity revealed that observers responded slower in the transfer-test than in the last training block in the Orientation group, $t(11) = 4.47$, $p < 0.001$, $r^2 = 0.64$, but not in the Color group, $t < 1$ (Fig. 6).

3.2.4. Transfer index

One sample t -test of transfer index compared to 0 (complete specificity) revealed that both the Color and the Orientation group

had a significant transfer effect, $t(11) = 5.42$, $p = 0.0001$, $r^2 = 0.72$, and $t(11) = 2.20$, $p = 0.024$, $r^2 = 0.30$. Indeed the fact that the transfer index score for each group was around 1 suggests a complete transfer of learning (Fig. 7A) and supports the binding-learning hypothesis (Fig. 7B).

3.3. Discussion

These findings indicate that learning completely transferred to the new target conjunction regardless of whether the test-target changed its color or its orientation. In addition, the transfer-test block resulted in longer RTs and more conservative criterion than the training blocks in the Orientation group, but not in the Color group. This effect may be due to the fact that the swapping of orientation (50–80°) is subtler than the swapping of colors alone (red to green) or the swapping of orientation and colors together (Experiment 1). This notion is supported by the relatively low performance during the pre-test example trials for the Orientation group (Table 1), which indicates that observers were less successful in identifying the change of orientation than the one in color. In any case, this RT and criterion differences did not correspond to a change in sensitivity, which remained the same between the last block of training and the transfer-test block.

Importantly, these results rule out the possibility that the specificity observed in the No-Exposure group in Experiment 1 was due to the number of conjunction combinations presented during training and/or the amount of learning. Here we show transfer of learning using the same number of conjunction combinations during training as in the No-exposure group. Moreover, in the Orientation group, observers improved by 0.96 d -prime during training. This improvement is similar to the amount of improvement observed in the No-exposure group in Experiment 1 (1 d -prime). However, whereas in the No-exposure group learning did not fully transfer to the test target, in the Orientation group performance remained the same between the last block of training and the test block. Overall, the results of Experiment 2 provide converging evidence for the conclusion that integration learning is restricted to the specific conjunction of specific features that were presented during training, but its persistent effects (transfer) are similar irrespective of whether the learned conjunction was initially targeted or suppressed.

4. Experiment 3

Long lasting persistence of perceptual learning is considered to reflect brain plasticity (e.g. Watanabe et al., 2002). However, with fast perceptual learning persistence had been shown for only few weeks (Fiorentini & Berardi, 1980). Recently we have shown that short training in a task that taxes spatial integration of features (i.e. crowding) can induce rapid and long lasting improvement (Yashar, Chen, & Carrasco, 2015). Here we tested whether the binding learning, as demonstrated in Experiment 1 and 2, is persistent for a long period of time by testing observers 5–16 months after training (without any additional training in between).

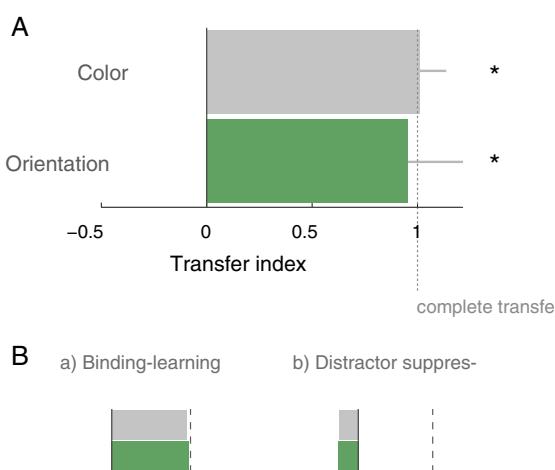


Fig. 7. (A) Mean transfer index for the Color and Orientation groups in Experiment 2. Complete transfer is indicated by $T = 1$ and complete specificity by $T = 0$. Error bars are within-subject standard errors (Morey, 2008). (B) The predicted results according to the two hypotheses: (a) binding-learning, and (b) distractors suppression.

4.1. Method

4.1.1. Observers

We repeatedly contacted all participants in Experiment 1 and Experiment 2 and retested all the ones that replied to our email as soon as they were available. Observers were paid for their participation. Sixteen observers from Experiments 1 and 2 – eleven observers from Experiment 1 (seven from the No-exposure group and four from the Exposure group) and five observers from Exper-

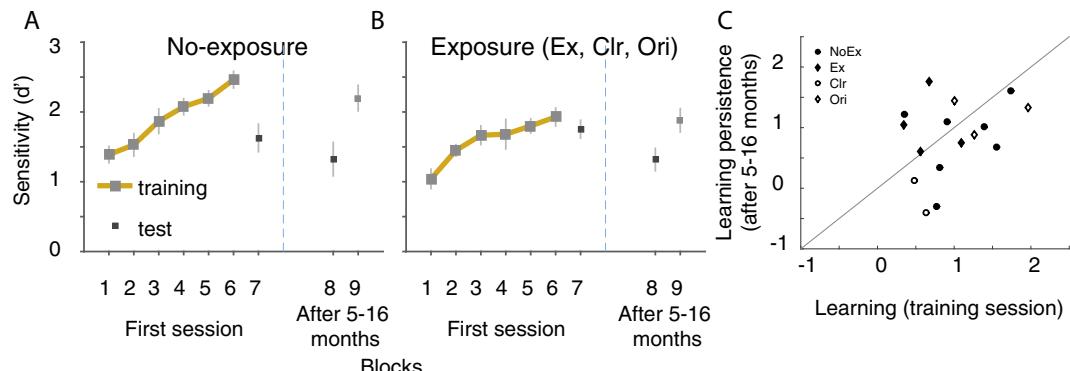


Fig. 8. Experiment 3. Mean sensitivity (d') as a function of training (blocks 1–6) transfer test (block 7) and the 5–16 months later follow-up session with the transfer test display (block 8) and the training display (block 9) from the No-exposure (A) and the Exposure Color and Orientation (B) groups. (C) Individual data for all four groups [NoEx = No-exposure, Ex = Exposure, Clr = Color, Ori = Orientation]. X-axis denotes learning within the training session (d' sixth block – d' first block). Y-axis denotes sensitivity for the trained stimulus in the follow-up session after 5–16 months (d' ninth block – d' first block). Error bars are within-subjects standard errors (Morey, 2008).

iment 2 (two from the Color group and three from the Orientation group) –participated in a follow-up session of two blocks.

4.1.2. Stimuli, procedure and design

The apparatus, stimulus, procedure and design were the same as in the observer's respective experiment. The first block was the observer's respective transfer block of Experiment 1 or 2 (according to the observer) and then its respective training block. Six observers were retested five to six months after the first session. Another 10 observers were retested 11–16 months after the first session.

4.2. Results

As indicated by the high performance in the example trials (pre-test and pre-training) observers had ample pre-knowledge of the training target and test target in both groups (Table 1). Fig. 8 depicts a plot of the learning transfer and delayed retest effects on sensitivity. To assess the persistence of learning an ANOVA was conducted with training block (the first training block vs. the follow-up training block) as a within-subjects factor, and the four training groups (E1-No-exposure, E1-Exposure, E2-Color and E2-Orientation) as a between-subjects factor. The main effect of training block was significant, $F(1, 12) = 37.34, p = 0.0001$. Neither the main effect of experiment group, $F < 1$, nor its interaction with training block, $F(3, 12) = 2.84, p > 0.8$, was significant, suggesting that learning was maintained over months and even a year after training. To assess the persistence of transfer, an ANOVA was conducted with training block (the last training block vs. the follow-up transfer block) as a within-subjects factor, and the four training groups as a between-subjects factor. None of the effects were significant, all $Fs < 1$. Because group did not interact with either the learning or the transfer effect, we further analyze the data by collapsing the data based on whether the transfer target was presented as a distractor during training; i.e., Experiment 1–Exposure group and Experiment 2 – Color and Orientation groups. For both the No-exposure ($n = 7$) and Exposure groups ($n = 9$), learning was maintained for the trained display. Paired comparisons (corrected for multiple comparisons) between the first training block and the follow-up block with the training display were significant both for the No-exposure, $t(6) = 3.38, p = 0.03, r^2 = 0.65$ and the Exposure groups, $t(8) = 3.75, p = 0.012, r^2 = 0.63$, indicating that short training can induce long lasting changes in feature conjunction. Individual data show learning persistence for all but two participants across groups (Fig. 8C). The training stimulus in the follow-up session was the same as the last training block for both

Exposure and No-exposure groups, both $t < 1.1$. Paired comparisons between the first training block and the follow-up block with the transfer display were not significant either for the No-exposure and the Exposure groups, all $ts < 1$, indicating that sustained learning does not transfer to the untrained target even when it was displayed as distractor during training.

4.3. Discussion

In both groups performance in the training display during the follow-up test (5–16 months after) was as high as the last training block during the training session (Fig. 8, block 6 vs. block 9). This finding indicates that learning was maintained for up to 16 months for both groups. Interestingly, unlike learning within the first training session, in both groups, maintained learning was specific to the trained target; it did not transfer to all presented conjunctions (Fig. 8B (Exposure group), block 6 vs. block 9). These findings indicate that (1) short training in conjunction tasks can induce a long lasting improvement, and (2) improvement during training generalizes to all presented stimuli, but long-term consolidation of learning is specific to the combined features of the target conjunction during training.

Note that the improvement during training in the follow-up No-exposure group (Fig. 8A) is noticeably higher than the improvement during training in the No-exposure group in Experiment 1 (Fig. 3 left panel). This is perhaps due to the fact that highly motivated observers are more likely to show up several months after training to participate in the follow-up test.

5. General discussion

This study is the first to show direct evidence for training-induced improvement in feature binding. A single and short session of training induced a substantial and long-lasting improvement of observers' ability to detect a target defined by a specific conjunction of a color and an orientation. Immediately after training this improvement transferred to different test targets as long as the same combination of feature conjunctions had been presented during training and test displays; regardless of whether that conjunction constituted only $\leq 9\%$ (Experiment 1, Exposure group) or 50% (Experiment 2) of the distractors. However, improvement did not transfer to a test target when the same colors and orientations were differently combined (Experiment 1, No-exposure group). In other words, when the test target was defined by a feature combination that had not been presented as either the target or a distractor during training, even though all training distractors

shared one feature with the new target, no transfer was found. These findings support the hypothesis that observers learn how to efficiently bind a specific conjunction of features, rather than merely learning how to better discriminate specific features per se (Fig. 2). Remarkably, learning can last for at least 16 months without additional training (Experiment 3), which reflects long-term plasticity. Interestingly, this long-lasting improvement was specific to the trained target conjunction in all training conditions, suggesting that task relevancy is necessary for long term consolidation of rapid feature binding learning.

The rapid presentation of the stimulus display (117 ms) prevents the deployment of endogenous (voluntary) attention, which takes about 300 ms (review by Carrasco, 2011), suggesting that the effect relates to the process of features binding per se rather than attentional control. Thus with a short training observers can become very efficient in integrating arbitrary features into objects with no deployment of endogenous attention.

The binding learning presented here differs from learning associated with selection processes. For example, perceptual learning can induce suppression of supra-threshold task irrelevant information (e.g., Paffen, Verstraten, & Vidnyánszky, 2008; Vidnyánszky & Sohn, 2005). Suppression of information also happens for very-short term effects in intertrial priming in visual search; i.e., the facilitation effect mediated by display repetition from trial to trial (see Kristjánsson & Campana, 2010 for review). Intertrial priming during conjunction search impairs detection when target and distractor are swapped (e.g., Kristjánsson et al., 2002), reflecting feature activation of target and inhibition and distractor (e.g., Lamy, Antebi, Aviani & Carmel, 2008; White, Rolfs, & Carrasco, 2013; Yashar & Lamy, 2010; Yashar & Lamy, 2011). In contrast to these suppression findings as a result of exposure, our findings demonstrate short-term learning that transfers to a new target even when the target had been a distractor (i.e. a to be ignored item) during training (Experiment 1, Exposure group and Experiment 2). The inconsistency between the current findings, and the findings showing suppression (e.g., Paffen et al., 2008; Vidnyánszky & Sohn, 2005) provides further indication that the learning effect demonstrated here does not reflect an improvement in the selection processes, but rather enhanced representation of the conjunction features presented during training.

Recently, Shibata, Sagi, and Watanabe (2014) proposed a model with two distinct stages of learning: a feature-based and a task-based plasticity. They propose that the former reflects changes in early perceptual areas related to the representation of basic features whereas the latter reflects changes in higher-level cognitive areas. Feature-based learning is demonstrated in the learning of the motion of sub-threshold, task-irrelevant stimuli (e.g., Seitz, Kim, & Watanabe, 2009; Watanabe et al., 2001). Task-based learning is demonstrated when learning is specific to the task relevant stimulus (e.g., Sagi, 2011 for review). Our findings show long-lasting learning that is task-based because learning was specific not only to the display conjunction but also to the task associated with that conjunction; i.e. whether it was a target or a distractor. However, our short-term learning generalized across all presented conjunctions regardless of whether they were to be detected (target) or ignored (distractor). Thus, the short term learning we found is not constrained by task.

Most studies that demonstrated long lasting persistence of perceptual learning used prolonged training over couple of days (e.g., Frank et al., 2014; Kami & Sagi, 1993; Watanabe et al., 2002; Yotsumoto, Watanabe, & Sasaki, 2008). For example, Frank et al. (2014) demonstrated that after 8 days of training observers improvement in a color/position conjunction search lasted for at least 9 months after training. Here we show the novel finding that a short session of conjunction training induces learning that persists for at least 5–15 months. This finding is in line with a recent

study showing that training under crowding conditions, that is, the failure to identify a peripheral object when it is surrounded by nearby objects, can lead to improvement that lasts for at least 8–12 months without additional training (Yashar et al., 2015). Taken together, our current and previous studies suggest that with various stimuli and tasks short training can induce long lasting changes in visual perception.

Specificity of perceptual learning is associated with the amount of training performed; whereas slow learning (after several sessions) is specific, fast learning (after one session) is more general (e.g., Kami & Sagi, 1993; see Sagi, 2011 for review). Here we show specificity that is not contingent on the amount of training but rather on consolidation. With the same amount of training, learning transferred when tested immediately after training, but became specific when tested after several months.

Finally, binding learning has the potential to explain people's ability to detect objects in a very brief display of complex natural scenes. The detection of real-life objects requires integration and binding of various features within a complex scene. Yet, people perform remarkably well at that task. The categorization of complex natural scenes can be as fast as 150 ms (Thorpe, Fize, & Marlot, 1996) or 100 ms (Crouzet, Kirchner, & Thorpe, 2010), and can occur with little or no attention (Li, VanRullen, Koch, & Perona, 2002; Peele, Fei-Fei, & Kastner, 2009). To have this ability observers need to quickly and efficiently bind various features within a complex scene. Indeed, adding the natural (or 'diagnostic') colors to a natural scene facilitates the early stage of scene categorization (Goffaux et al., 2005; Oliva & Schyns, 2000). Diagnostic colors, such as blue sky and green leaves, are in fact feature bindings that people often see in daily life. Our findings show that repeated exposure to feature combinations improves the ability of the visual system to integrate these features into objects. Thus the remarkable ability to categorize and detect natural objects and the involvement of diagnostic color in this process can be at least partially explained by fast and long lasting plasticity of the feature binding process.

A central issue in visual perception is how we learn to bind features into objects. This study provides new evidence showing that this process can be substantially facilitated with just a brief amount of training and that learned patterns may persist for extended periods of time. These findings imply binding-specific plasticity mechanisms responsible for integrating different features into an object, which may explain the high binding efficiency for discerning visually complex natural scenes.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.cognition.2016.05.019>.

References

- Adab, H. Z., & Vogels, R. (2011). Practicing coarse orientation discrimination improves orientation signals in macaque cortical area v4. *Current Biology*, 21 (19), 1661–1666.
- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, 387(6631), 401–406.

Ball, K., & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science*, 218(4573), 697–698.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, 51(13), 1484–1525.

Carrasco, M., Evert, D. L., Chang, I., & Katz, S. M. (1995). The eccentricity effect: Target eccentricity affects performance on conjunction searches. *Perception & Psychophysics*, 57(8), 1241–1261.

Carrasco, M., & McElree, B. (2001). Covert attention accelerates the rate of visual information processing. *Proceedings of the National Academy of Sciences*, 98(9), 5363–5367.

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.

Crist, R. E., Li, W., & Gilbert, C. D. (2001). Learning to see: Experience and attention in primary visual cortex. *Nature Neuroscience*, 4(5), 519–525.

Crouzet, S. M., Kirchner, H., & Thorpe, S. J. (2010). Fast saccades towards faces: Face detection in just 100 ms. *Journal of Vision*, 10(4), 1–17, 16.

Di Lollo, V. (2012). The feature-binding problem is an ill-posed problem. *Trends in Cognitive Sciences*, 16(6), 317–321.

Donovan, I., Szpiro, S., & Carrasco, M. (2015). Exogenous attention facilitates location transfer of perceptual learning. *Journal of Vision*, 15(10), 1–16, 11.

Fiorentini, A., & Bertini, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, 287, 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.

Giordano, A. M., McElree, B., & Carrasco, M. (2009). On the automaticity and flexibility of covert attention: A speed-accuracy trade-off analysis. *Journal of Vision*, 9(3), 30.

Goffaux, V., Jacques, C., Mouraux, A., Oliva, A., Schyns, P., & Rossion, B. (2005). Diagnostic colours contribute to the early stages of scene categorization: Behavioural and neurophysiological evidence. *Visual Cognition*, 12(6), 878–892.

Hung, S. C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *The Journal of Neuroscience*, 34(25), 8423–8431.

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.

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

Kristjánsson, Á., & Campana, G. (2010). Where perception meets memory: A review of repetition priming in visual search tasks. *Attention, Perception, & Psychophysics*, 72(1), 5–18.

Kristjánsson, Á., Wang, D., & Nakayama, K. (2002). The role of priming in conjunctive visual search. *Cognition*, 85(1), 37–52.

Lamy, D., Antebi, C., Aviani, N., & Carmel, T. (2008). Priming of pop-out provides reliable measures of target activation and distractor inhibition in selective attention. *Vision Research*, 48(1), 30–41.

Li, F. F., VanRullen, R., Koch, C., & Perona, P. (2002). Rapid natural scene categorization in the near absence of attention. *Proceedings of the National Academy of Sciences*, 99(14), 9596–9601.

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 of the United States of America*, 102(15), 5624–5629.

Morey, R. D. (2008). Confidence intervals from normalized data: A correction to Cousineau (2005). *Tutorials in Quantitative Methods for Psychology*, 4, 61–64.

Oliva, A., & Schyns, P. G. (2000). Diagnostic colors mediate scene recognition. *Cognitive Psychology*, 41(2), 176–210.

Paffen, C. L., Verstraten, F. A., & Vidnyánszky, Z. (2008). Attention-based perceptual learning increases binocular rivalry suppression of irrelevant visual features. *Journal of Vision*, 8(4), 25–25.

Peelen, M. V., Fei-Fei, L., & Kastner, S. (2009). Neural mechanisms of rapid natural scene categorization in human visual cortex. *Nature*, 460(7251), 94–97.

Prinzmetal, W., Presti, D. E., & Posner, M. I. (1986). Does attention affect visual feature integration? *Journal of Experimental Psychology: Human Perception and Performance*, 12(3), 361.

Robertson, L. C. (2003). Binding, spatial attention and perceptual awareness. *Nature Reviews Neuroscience*, 4(2), 93–102.

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

Schneider, W., Eschman, A., & Zuccolotto, A. (2002). E-Prime: User's guide. Psychology Software Incorporated.

Seitz, A. R., Kim, D., & Watanabe, T. (2009). Rewards evoke learning of unconsciously processed visual stimuli in adult humans. *Neuron*, 61(5), 700–707.

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, 18–28.

Su, Y., Lai, Y., Huang, W., Tan, W., Qu, Z., & Ding, Y. (2014). Short-term perceptual learning in visual conjunction search. *Journal of Experimental Psychology: Human Perception and Performance*, 40(4), 1415–1424.

Szpiro, S. F., & Carrasco, M. (2015). Exogenous attention enables perceptual learning. *Psychol. Sci.*, 1854–1862.

Szpiro, S. F., Sperling, M., & Carrasco, M. (2014). Perceptual learning modifies eye movements. *Journal of Vision*, 14(8), 1–13, 8.

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, 26(12), 520–522.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1), 97–136.

Vidnyánszky, Z., & Sohn, W. (2005). Learning to suppress task-irrelevant visual stimuli with attention. *Vision Research*, 45(6), 677–685.

Walsh, V., Ashbridge, E., & Cowey, A. (1998). Cortical plasticity in perceptual learning demonstrated by transcranial magnetic stimulation. *Neuropsychologia*, 36(1), 45–49.

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.

White, A. L., Rolfs, M., & Carrasco, M. (2013). Feature-based attention involuntarily and simultaneously improves visual performance across locations. *Journal of Vision*.

Wolfe, J. M. (2012). The binding problem lives on: Comment on Di Lollo. *Trends in Cognitive Sciences*, 16(6), 307.

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

Yashar, A., & Lamy, D. (2010). Intertrial repetition facilitates selection in time common mechanisms underlie spatial and temporal search. *Psychological Science*, 21(2), 243–251.

Yashar, A., & Lamy, D. (2011). Refining the dual-stage account of intertrial feature priming: Does motor response or response feature matter? *Attention, Perception, & Psychophysics*, 73(7), 2160–2167.

Yotsumoto, Y., Watanabe, T., & Sasaki, Y. (2008). Different dynamics of performance and brain activation in the time course of perceptual learning. *Neuron*, 57(6), 827–833.

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. *The Journal of Neuroscience*, 30(37), 12323–12328.