

Resetting capacity limitations revealed by long-lasting elimination of attentional blink through training

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As with other cognitive phenomena that are based upon the capacity limitations of visual processing, it is thought that attentional blink (AB) cannot be eliminated, even after extensive training. We report in this paper that just 1 h of specific attentional training can completely eliminate AB, and that this effect is robust enough to persist for a few months after training. Results of subsequent behavioral and functional magnetic resonance imaging (fMRI) experiments indicate that this learning effect is associated with improvements in temporal resolution, which are mainly due to processing in the prefrontal areas. Contrary to prior wisdom, we conclude that capacity limitations can be overcome by short-term training.

learning in temporal attention | color-salient training | plasticity

Visual information processing progresses hierarchically. In its early stages, the bulk of “raw” signals are processed in parallel. However, as signals are processed in higher stages, they become more abstract and cognitively meaningful, whereas the capacity of information processing becomes more limited in many respects, including visual short-term memory (1) and temporal attention (2). One of the best known phenomena that reflects the limited capacity of visual processing is attentional blink (AB), in which the identification of a second visual target (T2) is impaired in rapid serial visual presentation (RSVP) when that target is presented within 500 ms of the appearance of the first target (T1) (3–5). It is thought that AB occurs because the processing of T1 requires the full capacity of this portion of the visual system and does not allow for the processing of T2.

If capacity limits could be increased, processing efficiency may be greatly improved in some cognitive tasks. There have been a number of attempts to eliminate AB through repetitive practice (2, 6, 7). However, so far none of these attempts have been successful in eliminating AB. These failures have led to the belief that it is impossible to eliminate the capacity limit associated with AB. In the current study, however, we developed a simple, short-term training method with which the AB capacity limitation can be entirely overcome. We also found that this learning effect lasts for a few months after training. Further results from behavioral and fMRI studies suggest that this elimination of AB is associated with an improvement in temporal resolution correlated with processing in the prefrontal areas. Overall, these results suggest that capacity limitations can be overcome by simple, short-term training.

Results

To eliminate AB, we drew attention to T2 during training with a salient color. That is, T2 had a different color from all of the other items of the RSVP task. T2 thus captured the subjects' attention, such that it was easily identified and no longer subject to AB. We addressed the question as to whether repeating this task would bring about an improvement in the capacity of temporal attention.

Experiment 1: Color-Salient Training Effect. Experiment 1 explores whether training with a salient T2 can eliminate AB. We conducted experiment 1 for three successive days with 10 subjects. Each day before training we measured AB with a RSVP task in which the subjects were asked to identify one or two digits presented among letter distractors. All items in the RSVP stream were presented in a monochrome white color. To measure AB, we compared the accuracy of T2 identification over two conditions (Fig. 1A). Because AB has been shown to exclusively affect T2 when presented within 500 ms of T1, we used one condition with a stimulus onset asynchrony (SOA) of less than 500 ms and another condition with a SOA of greater than 500 ms. In the short SOA condition, a single intervening distractor separated T2 from T1 (i.e., T2 was presented after T1 and a single intervening distractor, or at “lag 2”). Each item of the RSVP task was displayed for 100 ms, and thus T2 was presented 200 ms after the appearance of T1 in the short SOA condition. Because 200 ms is within the AB period, T2 should be difficult to identify in the short SOA condition. In the long SOA condition, T2 was at lag 6 (600 ms SOA), which was outside the AB period. A significant difference in performance between these two conditions would demonstrate the effects of AB.

During training, a modified RSVP task was used (Fig. 1B). Although T2 was always presented at lag 2 (which corresponded to the short SOA condition in the before-training session), T2 was given a salient color (red), allowing it to stand out from the otherwise monochrome (white) items of the RSVP stream. That is, the salient color attracted attention to T2 and facilitated its identification. Subjects performed this “color-salient” RSVP training task 450 times on each of the 3 d.

Surprisingly, after a single day of training with the salient T2, AB was eliminated even for the normal, entirely monochrome RSVP task (Fig. 2A). The significant performance difference between the short and long SOA conditions [paired *t* test, $t(9) = 4.91$, $P < 0.001$] that was present before training on the first day of the experiment was eliminated on the second day [paired *t* test, $t(9) = 1.60$, $P = 0.14$] and the third day [paired *t* test, $t(9) = 0.95$, $P = 0.36$]. Because the salient T2 was used only during training, the elimination of AB in the before-training session on the second and third days was not due to the salient color.

Experiment 2: Durability of the Color-Salient Training Effect. We next tested the durability of this learning effect. In experiment 2, we recalled five of the subjects who had participated in experiment 1 to measure AB again. The average interval between their initial participation and the retest was 2.5 mo (range of 1.5–4.5 mo).

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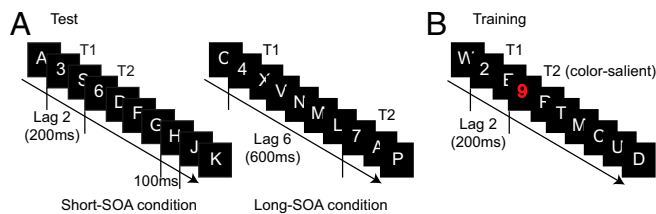


Fig. 1. Depiction of RSVP used in tests and training in experiment 1. (A) RSVP procedures when AB was measured. There were two conditions: the short SOA condition (Left) and the long SOA condition (Right). In the short SOA condition, T2 was presented at lag 2 (200 ms SOA). In the long SOA condition, T2 was at lag 6 (600 ms SOA). (B) RSVP procedure of the color-salient training. T2 at lag 2 was made salient by coloring the digit red.

Despite the long interval between tests, there was no significant difference between the short and long SOA conditions (Fig. 2B). In other words, the AB effect that was found for these subjects on the first day [paired *t* test, $t(4) = 3.22$, $P = 0.03$] was removed not only on the second day [paired *t* test, $t(4) = 0.61$, $P = 0.57$] and on the third day [paired *t* test, $t(4) = 1.16$, $P = 0.31$] of experiment 1, but also on this fourth, follow-up day, which took place several months after the final day of experiment 1 [paired *t* test, $t(4) = 1.71$, $P = 0.16$]. Thus, we conclude that the learning effect is durable and long lasting.

Experiment 3: Training Without a Color-Salient T2. This learning effect occurred only when the T2 within the AB period was made salient during training. In experiment 3, T2 was not color salient during training, but otherwise the procedure was identical to that

of experiment 1. Six new subjects participated in this experiment. AB was clearly observed on each day of this experiment [on the first day, paired *t* test, $t(5) = 4.00$, $P = 0.01$; on the second day, paired *t* test, $t(5) = 4.10$, $P < 0.01$; on the third, paired *t* test, $t(5) = 4.97$, $P < 0.01$; Fig. 2C]. The results indicate that for AB to be eliminated, T2 has to be made salient during training.

Experiment 4: Disassociation Between a Salient Color and T2. To explore the necessity of pairing a salient color with T2 in the RSVP stream, we conducted an experiment during training of which T2 was presented at various lags, whereas the item at lag 2 was always salient, regardless of whether this item was a target or a distractor. Eight new subjects participated in this experiment. AB was observed on all days of the experiment [paired *t* test, on the first day, $t(7) = 3.22$, $P = 0.015$; on the second day, $t(7) = 3.40$, $P = 0.011$; on the third day, $t(7) = 3.26$, $P = 0.014$; Fig. 2D]. The results of experiments 3 and 4 together indicate that AB is eliminated only when T2 is consistently attended to during training.

Experiment 5: Nonspecificity to a Trained Lag. The learning effect we have reported thus far is based on improvement in identification of T2 with a specific trained lag (lag 2). We might then ask, “Is this training improvement lag-specific?” In experiment 5, before and after 2 d of training (720 trials a day) in which color-salient T2 was always presented at lag 2, six subjects conducted a normal RSVP task in which T2 was presented at various lags ranging from lag 1 to lag 6.

AB was clearly observed before training (pretest). Subject performance was significantly affected by lag position [a main effect of lags in one-way repeated-measure ANOVA, $F(5,25) = 7.64$, $P < 0.001$]; performance was much poorer when T2 was

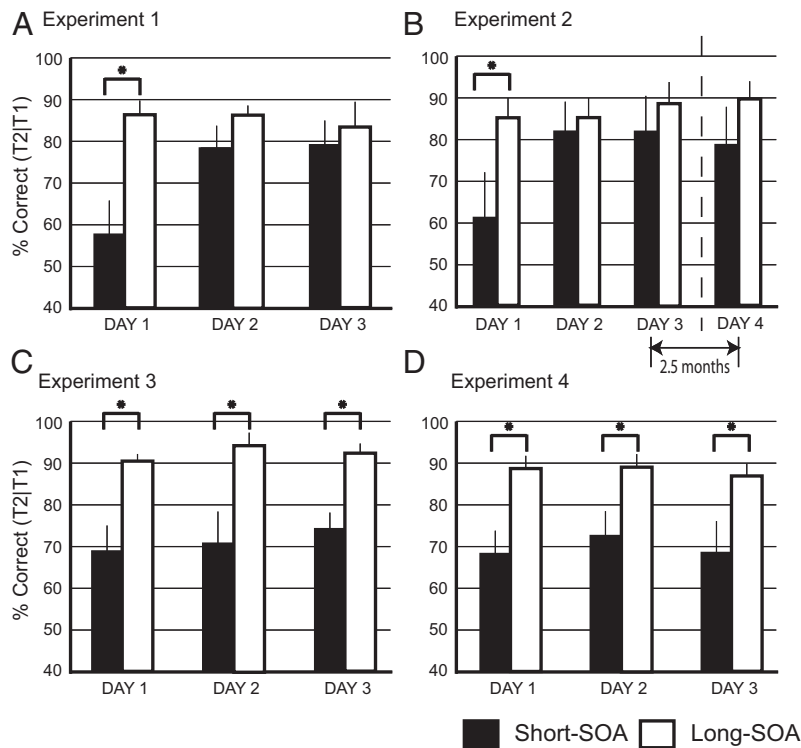


Fig. 2. Results of experiments 1–4. Mean percentages (\pm SEM) of T2 accuracy concurrent with correct T1 response (T2/T1) for each condition are shown. Degree of AB was determined by testing differences in accuracy between the short and long SOA conditions. AB was measured twice per day, before and after the salient training, but here we report only the performance measured before the training. For further discussion, see *SI Experimental Procedures* and Fig. S1. (A) Results of experiment 1. (B) Results of experiment 2. Results of days 1, 2, and 3 are from experiment 1; the result of day 4 is from an additional test that was conducted, on average, 2.5 mo after the conclusion of experiment 1 without any further training during the interval. (C) Results of experiment 3. (D) Results of experiment 4. * $P < 0.05$.

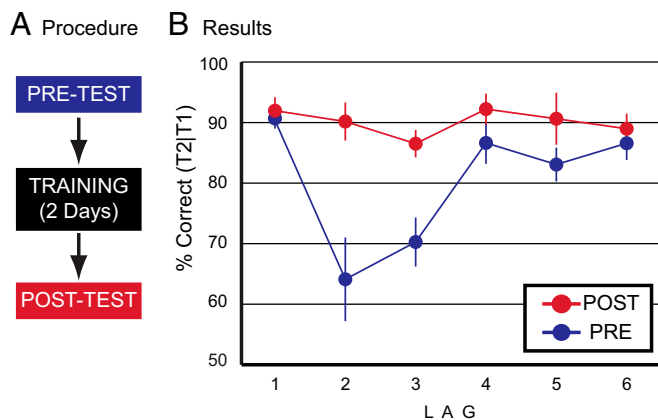


Fig. 3. Procedure and results of experiment 5. (A) Procedure. A whole experiment consisted of one pretest session, two training sessions, and one posttest session, in that order. (B) Results. Mean percentages (\pm SEM) of T2 accuracy concurrent with correct T1 response (T2/T1) for each condition are depicted.

presented at shorter lags than at longer lags. However, these differences were not observed after training [posttest; a main effect of lags in one-way repeated-measure ANOVA, $F(5,25) = 1.73, P = 0.16$]. This result indicates that AB was eliminated even at untrained lags, suggesting that color-salient training effects are not specific to a trained lag (Fig. 3).

Learning effects related to lower-level visual processing often show a high degree of spatial and temporal specificity (8, 9). The nonspecific learning effect demonstrated here is inconsistent with lower-level learning and implies that elimination of AB may be related to changes in higher-level processing.

There are at least two possible mechanisms that could underlie the elimination of AB. Elimination of AB could be due to an improvement of overall information processing capacity during RSVP. Alternately, the elimination of AB could be the result of strategic changes, rather than changes in capacity itself. Repeated performance of RSVP with a salient T2 at a fixed lag could prime observers to identify T2 at that lag. However, if such a strategy were the underlying cause of the training effect, it would induce a tradeoff: observers would demonstrate poor performance when T2 was presented at untrained lags. Therefore, the nonspecificity of experiment 5 suggests that the elimination of AB is due to an increase in overall information processing capacity during RSVP.

Experiment 6: Increase of Temporal Resolution Due to Color-Salient Training. One possible explanation for this overall capacity increase is that our salient training may give rise to long-lasting improvement in temporal resolution, the ability to discriminate between visual stimuli in a rapid sequence (Fig. S2). To test this hypothesis, in experiment 6a we examined whether the salient training induced an improvement of performance in a masking task, in which subjects were asked to identify a target presented immediately before or after a mask. Ten subjects participated in this experiment. The masking tests were conducted before and after 2 d of salient training (720 trials a day). Each trial consisted of the sequential presentation of two items, a target digit and a letter mask. Presentations of target and mask were separated by various SOAs (from -36 ms to 72 ms). After training of the RSVP task with a color-salient T2, performance in the masking test improved significantly [a main effect of training in two-way repeated-measure ANOVA with training and SOAs, $F(1, 9) = 11.99, P = 0.007$; Fig. S34]. In experiment 6b, in which training occurred without color-salient T2 (seven new subjects), no significant improvement was observed [a main effect of training

in two-way repeated-measure ANOVA with training and SOAs, $F(1, 6) = 1.48, P = 0.27$; Fig. S3B]. These results are in accord with the hypothesis that salient training leads to enhancements in temporal resolution.

Experiment 7: Neural Correlates of the Color-Salient Training Effect. There are at least two explanations for the improvement of temporal resolution in the RSVP task. One possibility, which we refer to here as “processing-based improvement,” is that temporal resolution is increased as a result of improvements in processing each individual item in the RSVP stream. It has been suggested that AB occurs due to conflicts between the processing of T1 and T2. T2 may not be identified if it is presented while T1 is being processed, because most of the observer’s attentional resources are allocated towards T1 processing (Fig. 4A). If salient training improves the processing of a single item, especially T1, the processing of T1 may then be completed before T2 is presented within the AB period. In other words, the processing of T1 and T2 no longer overlap each other, as in long SOA conditions (Fig. 4B).

The other possibility, which we refer to as “attention-based improvement,” is that this training effect is related to changes in attentional regulation patterns, rather than in the processing of individual items. A recent study has suggested that AB is due to a temporary loss of attentional control (10). The attentional control mechanism, in which targets are selected for processing and distractors are inhibited, does not function properly while T1 is being processed. If color-salient training improves attentional control, then T2 presented within the AB period should be successfully identified even if T2 processing overlaps with T1 processing. If that is the case, successful identification of T2 within the AB period after salient training would show different processing characteristics compared to identification of T2 outside the AB period (Fig. 4C).

To determine which possibility is more likely, we conducted experiment 7 with nine subjects using a functional magnetic

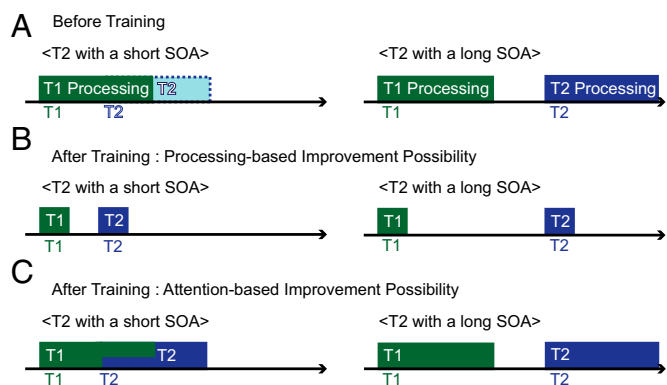


Fig. 4. Illustrations of target processing in the pretest and after training, according to two alternate hypotheses. (A) Processing before training (pretest). T2 with a short SOA (Left) cannot be identified because most of the observer’s resources are allocated to T1 processing, whereas T2 with a long SOA (Right) can easily be identified, because there is no conflict with T1 processing. (B) Processing after training according to the processing-based improvement hypothesis. T2 with a short SOA can be identified because the salient training shortens T1 processing time, which is now completed even before the onset of T2 with a short SOA. Thus, T2 with a short SOA (Left) is outside the AB window, as is the case for T2 with a long SOA (Right). (C) Processing after training according to the attention-based improvement hypothesis. T2 with a short SOA is successfully identified due to improved attentional control, which enhances signals from targets (including T2) and inhibits signals from distractors. As a result, T2 can be identified while T1 is still being processed.

resonance imaging (fMRI) technique. Before and after 2 d of salient training (720 trials a day), AB was measured in the short SOA and long SOA conditions, as in experiment 1. During observer performance we measured blood-oxygen-level-dependent (BOLD) signals in multiple brain areas: V1 and three areas that are reportedly involved in AB (11): intraparietal sulcus (IPS), anterior cingulate cortex (AC), and dorsolateral prefrontal cortex (DLPFC).

Using multivoxel pattern analysis (12–15) we calculated correlation coefficients of the BOLD signal patterns between conditions and then investigated changes in the correlations induced by training. If the salient training gave rise to processing-based improvements, T2 of the short SOA condition would be processed without any conflict from the processing of T1, similar to processing in the long SOA condition (Fig. 4B). Thus, after training we would expect the neural activity pattern of the short SOA condition to become similar to that of the long SOA condition. The correlation coefficient of BOLD signals patterns between the short SOA and long SOA conditions should be higher after training.

On the other hand, if the learning effect is related to attention-based improvements, T2 of the short SOA condition would be processed in a different way from T2 of the long SOA condition because of the overlap with T1 processing (Fig. 4C). Thus, higher correlation between the two conditions would not be expected after training.

After training, the behavioral performance between the short and long SOA conditions became similar, once again demonstrating the elimination of AB (paired t test, $t(8) = 0.01$, $P = 0.99$). The correlation between the short and long SOA conditions significantly or marginally decreased in the three regions of interest, DLPFC (paired t test, $t(8) = 4.03$, $P = 0.003$, uncorrected), IPS (paired t test, $t(8) = 2.01$, $P = 0.07$, uncorrected), and AC (paired t test, $t(8) = 1.79$, $P = 0.10$, uncorrected; Fig. 5). Correlation decrease was most pronounced in DLPFC. However, V1 showed no change in correlations (paired t test, $t(8) = 0.38$, $P = 0.71$, uncorrected). These results support the attention-based improvement hypothesis. Our earlier findings showed that the color-salient learning effect was related to an increase of temporal resolution. Taken together, these results imply that learning that overcomes deficits in temporal attention occurs due

to an improvement of temporal resolution resulting from top-down attentional signals.

Discussion

In this series of experiments we found that the robust phenomenon, AB, can be totally ameliorated with short periods of color-salient training (the shortest being 1 d with 450 trials), and that this effect persists for a few months, even without any further training. Reduction of AB has been reported in several recent studies. However, most of these reductions were obtained through some manipulation of either RSVP displays or RSVP tasks. For example, AB could be attenuated when task-irrelevant visual motion or flicker was added (16). When a temporal cue for T2 was provided, AB magnitude was reduced (17). In the current study, manipulation was only used during training in which a color-salient T2 was presented. After this training, subjects could identify T2 within the AB period even though T2 was no longer salient. Thus, AB was totally eliminated even in normal RSVP displays where no color saliency manipulation was present.

The elimination of AB in this current study does not seem compatible with previous studies that have failed to eliminate AB with practice (2, 6, 7). The most significant difference between those studies and the current study is the use of a modified task with a color-salient T2 during training, whereas previous studies have attempted to remove AB simply by repetitive practice of a normal RSVP task. The use of a color-salient T2 is essential. As demonstrated in experiment 3, training without a color-salient T2 has no effect on AB. However, color by itself does not influence AB. When both targets are defined by color (e.g., subjects are asked to report two white target letters presented among black distractor letters), AB still occurs (18). In the current study, however, color is used to make T2 salient, not to define the features of both targets. During training, T2 is given a unique color in the RSVP stream (T1 shares the same color as distractors). This salient T2 captures subjects' attention and enables the target's successful identification. This is consistent with the results of previous studies that attempt to manipulate subjects' attention. For example, when a temporal cue indicating the serial position of T2 is provided, subjects can then pay greater attention to T2, thus reducing AB (17).

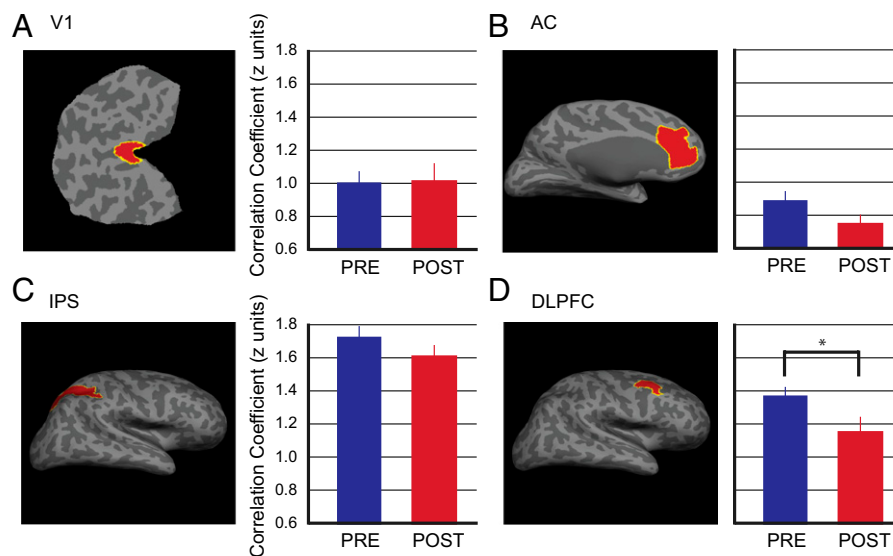


Fig. 5. Results of multivoxel pattern analyses in four cortical areas in experiment 7. (A) V1, (B) AC, anterior cingulate, (C) IPS, intraparietal sulcus, and (D) DLPFC, dorsolateral prefrontal cortex. Mean correlation coefficients (\pm SEM) between fMRI signal patterns in the short and long SOA conditions are shown. A Fisher transformation was applied to these correlation coefficients. * $P < 0.05$.

The salient color of T2 used during training may induce a strong learning effect on AB. First, repeated exposure of the salient T2, which captures the subjects' attention, may lead to direct changes of a temporal attention mechanism. Second, subjects can identify T2 more easily due to T2 being color salient. A higher success rate may increase the magnitude of the learning effect because behavioral success may function as an internal reward, which facilitates learning (19, 20).

Although we chose to use a color-salient T2 during training, it is possible that other types of cues could induce the elimination of AB. Most subjects reported that they observed not only color-salient target digits but also color-salient distractor letters that were not actually presented. This seems to be due to misbinding of features and suggests that the salient color works at least partially as a temporal marker that attracts subjects' attention, rather than an object-bound cue.

The results of our experiments support a model in which color-salient training improves attentional control mechanisms, which involve the selection of targets and inhibition of distractors. However, these results could alternately be explained with perceptual factors. For instance, subjects could have developed more precise target templates, a training effect that would be difficult to disentangle from attentional improvements. In the current study, only eight digits were used as targets both in training and tests, and were presented repeatedly in an identical form. This (perceptual) limitation might facilitate formation of templates for targets and easier template matching (with fewer resources). This advanced template matching might result in improved attentional control, whereas the processing time of the targets themselves would not change. There is some existing work suggesting that attentional limitations can be altered through perceptual learning (21). Although the results of experiments 5 and 7 suggest changes in higher-level processing rather than lower perceptual level processing, an exploration of the effects of perceptual factors on attentional control in these contexts would make for an interesting future study. Manipulation of perceptual similarity between training and tests would provide an appropriate answer to these questions.

Training-induced elimination of AB may seem similar to a previous study that demonstrated reduced AB after 10 d of training with a video game (22). However, because the previous study focused on the training effects of video games it was different from the current study in several important ways. First, the study did not explore the underlying mechanism of the training effect and instead focused only on performance improvements during the RSVP task. The researchers acknowledged that their results could not clarify whether the training effect was due to faster target processing or improved attentional mechanisms. Second, the previous study used a modified RSVP task that departed significantly from the standard task paradigm. In their experiment, subjects were asked to identify T1 and then to detect T2. This task was a combination of two attentional phenomena, AB and task switching, which have different characteristics. The cost of switching tasks was most pronounced when the two targets were temporally adjacent, and AB did not occur in this case. Thus, it was not clear whether these results were due to reduction of AB or improvement in task switching. Finally, whereas the study's results showed a significant improvement in the modified RSVP task, poor performance was still observed when T2 was presented with a short SOA. The study failed to remove AB even after 10 d of training, although it did show reduction of AB.

Although the current study focused on learning effects related to AB, rather than AB itself, our results have several important implications for its underlying mechanisms. It has been proposed that AB reflects a loss of information at a high-level, post-perceptual stage of information processing (23). The AB elimination effect we report here also implies changes in higher-level

processing. In the fMRI experiment, our training induced changes in higher areas such as IPS and AC, and most strongly in DLPFC. These results indicate that the elimination of AB is associated with an improvement in attentional control, consistent with the hypothesis that AB occurs due to a failure of attentional control (10).

Training with a color-salient T2 induced the elimination of AB, and this effect persisted for several months after the initial training. The training effect's nonspecificity to a trained serial position suggests that this learning induces changes in higher-level processing. The results of the masking and the fMRI experiment are in accord with the hypothesis that the learning effect is due to long-term improvements of temporal resolution, which are related to changes in prefrontal areas involving attentional control. It also suggests that deficits in temporal attention can be overcome by very short-term training regimens, which promote long-term changes in attentional regulation patterns.

Experimental Procedures

A total of 48 subjects had normal or corrected-to-normal visual acuity and were naïve as to the purpose of the study. All subjects gave informed written consent approved by the Boston University Institutional Review Board or the Massachusetts General Hospital Human Resource Committee. (Additional information is available in *S1 Experimental Procedures*.)

Basic RSVP Task. Eight single digits (0 and 1 were omitted to avoid confusion) and 22 uppercase letters (excluding B, I, O, and Q) were used. In each trial, a sequence of 10 items consisting of one-digit target and nine-letter distractors or two digits and eight letters was presented. The items were randomly selected in each trial and no item was shown twice in one trial. The sequence of items was presented within a 1.4° diameter white circular frame at the center of the screen. Each item was presented for 100 ms and subtended 0.4° by 0.6° of visual angle. All items were white and presented on a black background (Fig. 1).

Two RSVP conditions were used. In the short SOA condition, T2 was consistently presented at lag 2. In the long SOA condition, T2 was presented at lag 6. In both conditions, T1 was the second item of the sequence (serial position 2).

Previous research has shown that when observers develop expectations about the frequency of targets in the stream, AB is reduced (17). Thus, to minimize the effects of expectation, a one-target condition was also used, in which only one digit was presented. These functioned as catch trials and were not included in formal analyses and results. There were 30 trials per condition. All trials were randomly presented.

The experiment was self-paced. Subjects started each trial by pressing any key on the keyboard. An empty circular frame appeared for 200 ms, then the RSVP sequence was presented within the circle. After the presentation of the sequence, subjects were asked to report one or two numbers that they observed by pressing the corresponding number key. (Subjects were instructed that there would be either one or two numbers in RSVP. If they saw only one number, they would report only one number, and if they saw two numbers, they would report both of them.)

In experiment 5, T1 was presented at serial position 2 or 3. In addition, six steps of lags between the two targets, from lag 1 (100 ms SOA) to lag 6 (600 ms SOA), were used, in contrast to the two lags in the basic RSVP task. There were 40 trials per condition, in addition to 40 catch trials with only a single target, for a total of 280 trials.

In experiment 7, only four digits (from 2 to 5) were used as targets so that subjects could report targets more easily via a button box in a scanner. Each condition had 60 trials, for a total of 180 trials. There were five runs, each of which lasted 288 s. An event-related design was used and trial sequences were optimized with OptSeq software (<http://surfer.nmr.mgh.harvard.edu/optseq>). This experiment was not self-paced. After the presentation of the RSVP display, subjects had up to 3 s to report the targets by pressing buttons. Then the next trial automatically began according to a scheduled sequence.

Color-Salient Training. The procedure was identical to that of the basic RSVP task, with some exceptions. In all trials, T1 was constantly presented at serial position 2 and T2 at serial position 4 (lag 2). This procedure corresponded to the short SOA condition of the basic RSVP task. However, T2 was always made salient by displaying it in red, whereas all of the other items, including T1, were white (Fig. 1B). There were 450 trials (experiment 1) or 720 trials (experiments 5–7) per day.

During training of experiment 4, there were three RSVP conditions that corresponded to the one target, the short SOA, or the long SOA conditions in the basic RSVP task. The item at serial position 4, corresponding to lag 2, was colored red, regardless of whether the item was a digit (target) or a letter (distractor). There were 150 trials per condition, for a total of 450 trials.

Masking Task (Experiment 6). Each trial consisted of two items, a target digit and a letter distractor. Used items were identical to the items in the basic RSVP tasks. The two items were presented at the center of the screen in sequence, after a 400-ms exposure to a fixation cross. Distractors were presented at 10 SOAs: -36 , -24 , -12 , 0 , 12 , 24 , 36 , 48 , 60 , and 72 ms. A negative SOA refers to a trial in which a distractor appeared before a target, whereas a positive SOA indicates a trial in which a distractor appeared after a target. Because both a target and a distractor were presented for 36 ms, their presentations had the potential to overlap and superimpose on each other. There were 25 trials per each SOA, for a total of 250 trials.

Image Acquisition. Subjects were scanned in a 3T scanner (Siemens; Trio) with a head coil. Functional MR images were acquired using gradient echo planar imaging (EPI) sequence for measurement of BOLD signals. For the RSVP task, 33 contiguous slices [repetition time (TR) = 2 s, echo delay time (TE) = 30 ms, flip angle = 90° , voxel size = $3 \times 3 \times 3.5$ mm³] oriented parallel to the anterior commissure (AC)–posterior commissure (PC) plane were acquired, covering the entire brain. For the retinotopy measurement used to localize V1, 25 contiguous slices (TR = 2 s, TE = 30 ms, flip angle = 90° , voxel size = $3 \times 3 \times 3$ mm³) oriented orthogonal to the calcarine sulcus were acquired to cover the occipital cortex. T1-weighted MR images (MP-RAGE; TR = 2.531 s, TE = 3.28 ms, flip angle = 7° , 256 slices, voxel size = $1.3 \times 1.3 \times 1$ mm³, resliced during analysis to 1 mm³) were used in subsequent reconstruction of the cortex in flattened format (24, 25).

Regions of Interest (ROIs). We focused on V1 in the visual cortex and the three cortical areas known to be related to AB, which include IPS, AC, and DLPFC (11). V1 was localized individually in a separate fMRI session that used a standard flickering checkerboard pattern (26, 27). (The actual analysis used the data from a partial region of V1, rather than the entire region of V1, which corresponded to the visual area where the stimulus was presented.) IPS and AC were defined using an automated surface-based parcellation method (28), and DLPFC was defined in the middle frontal gyrus according to cytoarchitectural criteria (29). For all ROIs, left and right hemispheres were merged.

fMRI Data Analysis. Data were analyzed with FS-FAST and FreeSurfer software (<http://surfer.nmr.mgh.harvard.edu>). All functional images were motion corrected (30) and registered to the individual anatomically reconstructed brain. Signal intensity of functional images was normalized individually across runs. Spatial smoothing was applied only for retinotopy data. For each voxel, estimated signal amplitude and its t value were computed on the basis of a univariate general linear model. Contrasts of each condition were modeled separately.

Multivoxel pattern analysis (12–15) was used to explore changes in the similarities of neural activity patterns among conditions after training. With t values of each condition obtained across the voxels of each ROI for each subject on each day, correlation coefficients were calculated between two critical conditions, the short and long SOA conditions.

These correlation coefficients were then Fisher transformed before further analysis: $0.5 \ln[(1 + r)/(1 - r)]$.

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