

# Effect of spatial distance to the task stimulus on task-irrelevant perceptual learning of static Gabors

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It was previously shown that sensitivity improvements to a task-irrelevant motion direction can be obtained when it is presented in concurrence with observers' performance of an attended task (Watanabe, Náñez, & Sasaki, 2001; Seitz & Watanabe, 2003). To test whether this task-irrelevant perceptual learning (TIPL) is specific for motion and to clarify the relationships between the observer's task and the resultant TIPL, we investigated the spatial profile of the sensitivity enhancement for a static task-irrelevant feature. During the training period, participants performed an attentionally demanding character identification task at one location while subthreshold, static, Gabor patches, which were masked in noise, were presented at different locations in the visual field. Subjects' sensitivity to the Gabors was compared between the pre- and post-training tests. First, we found that TIPL extends to learning of static visual stimuli. Thus, TIPL is not a specialized process to motion stimuli. As to the effect of spatial location, the largest improvement was found for the Gabors presented in closest proximity to the task. These data indicate that the learning of the task-irrelevant visual feature depends significantly on the task location, with a gradual attenuation according to the spatial distance between them. These findings give further insights into the mechanism of perceptual learning.

## Introduction

It is well-established that with training adults can show significant improvements in various perceptual tasks (Fahle, & Poggio, 2002), such learning effects are called perceptual learning (PL). PL has been found to be highly specific to basic stimulus attributes, such as retinotopic location, angle of orientation, direction of motion, and even to the eye of training (Doshier & Lu, 1998; Ahissar & Hochstein, 1993; Poggio, Fahle, & Edelman, 1992; Schoups, Vogels, Qian, & Orban, 2001; Ball & Sekuler, 1982; Fiorentini & Berardi, 1980; McKee & Westheimer, 1978; Herzog & Fahle, 1999). For example, in some cases learning at one location, or of one orientation, does not transfer to another location or orientation.

Until recently, PL was thought to require attention to be directed to the learned visual feature during training. However, a series of studies revealed the phenomenon of task-irrelevant perceptual learning (TIPL), where the sensitivity improvements develop without attentional focus towards the learned visual feature (Watanabe, Náñez, & Sasaki, 2001; Ludwig & Skrandies, 2002; Seitz & Watanabe, 2003; Dinse, Ragert, Pleger, Schwenkreis, & Tegenthoff,

2003; Seitz & Watanabe, 2005; Seitz, Náñez, Holloway, Koyama, & Watanabe, 2005; Seitz, Lefebvre, Watanabe, & Jolicoeur, 2005; Amitay, Irwin, & Moore, 2006). For instance, Seitz and Watanabe (2003) reported an improvement in sensitivity specific to task-irrelevant motion stimuli that were subliminally presented in temporal correlation with the target stimuli of the subject's main task. These results have led to a model of PL that suggests that a featurally non-specific learning signal, which is triggered by successfully detecting the task targets, results not only in learning of task-relevant stimuli, but also in learning of task-irrelevant stimuli (Seitz & Watanabe, 2005).

While results of TIPL are highly suggestive of the existence of a featurally non-specific task-driven learning signal, we know very little regarding the properties of this signal. To better understand the signal, in the present studies, we investigate two questions regarding TIPL. First, is there any limitation to the spatial extent of TIPL? Second, is TIPL a specialized phenomenon related to processing of motion stimuli (used in previous studies of TIPL) or will TIPL hold true for other stimulus features, such as the orientation of a static Gabor stimulus?

To explore the spatial aspect and generality of TIPL, we presented subthreshold Gabor patches, which were spatially masked in noise (See Figure 1a), at different spatial locations while the subject performed an attentionally demanding character identification task. Our results confirm that TIPL generalizes to static orientation stimuli and suggest that there is a spatial restriction to the learning of these task-irrelevant stimuli.

## Experiment 1

In the first experiment, we examined the effect of task location along a horizontal axis in the visual field (Figure 2). TIPL was compared between two locations; one close and the other distant to the task. Based on classical results of spatial and orientation specificity of PL we investigated how learning under different conditions develops at the same time in a within-subject design. We measured performance improvement at different spatial locations and orientations independently, and evaluated the effect of the distance from the task-relevant stimuli by comparing changes in performance across conditions.

## Participants

Seven subjects (4 female and 3 male, age range 18-35 years), who were naïve as to the purpose of the study, participated and received payment for their completion of the experiment.

## Apparatus

The stimuli were presented using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for MATLAB® (The MathWorks, Natick, MA) on a Macintosh G4 computer. The stimuli appeared on a Radius 21" CRT monitor connected to the computer, with a resolution of 1600 by 1200 pixels and a refresh rate of 60 Hz. The view distance was 0.76 m and the pixel size was 1.13 arcmin. A chin rest was used to maintain the subject's head position. The subjects used a computer keyboard to make responses.

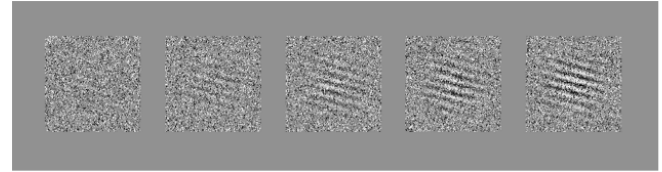
Eye movements were measured for some subjects during the training sessions using ViewPoint EyeTracker® system (Arrington Research, Scottsdale, AZ). This eye tracking system uses infrared video that has 0.15 deg spatial and 60 Hz temporal resolutions.

## Stimuli

The task-irrelevant stimuli were static Gabor patches that were superimposed on a background that was filled with spatial white noise (Figure 1a). We adopted Gabors with static background noise because they are in many ways analogous to the motion stimuli we have used in previous studies (Watanabe, Náñez, & Sasaki, 2001; Seitz & Watanabe, 2003). Also, in pilot experiments we found that this stimulus yielded more gradual psychometric functions and more within and across subject consistency than those ob-

tained with contrast modulated Gabors in the absence of background noise. Spatial frequency of the Gabors was either 0.5 cycles/deg or 5.0 cycles/deg (counterbalanced across trials), and the sigma of its Gaussian factor was 1.0

**a**



← Lower Contrast Higher Contrast →

**b**



Figure 1. a. Example of Gabor patches on random dot noise background with different Gabor contrasts. b. The phases of Experiments 1 and 2. Each subject performed pre- and post-tests for measuring Gabor sensitivity, before and after seven day training sessions, respectively.

deg. Two spatial frequencies were used so that cells tuned to a wide range of spatial frequencies would be stimulated and could potentially contribute to effects of learning. Results showed no systematic differences between the two spatial frequencies used (no significant difference in average performance in the pre-test;  $p=.199$ , paired  $t$ -test).

The noisy Gabor images were created by randomly selecting 20% of pixels from the Gabor image and 80% of pixels from the noise image. The background noise was generated from a sinusoidal luminance distribution with the exception that 20% of the pixels (same as signal-to-noise ratio of the Gabor) were chosen to be gray. In this way, the statistics of the luminance distributions were preserved between the Gabor and the background, so that there were no texture elements that could distinguish the Gabor patch from the noise field when the contrast of the Gabor was brought to 0%. The mean background luminance was 33  $\text{cd}/\text{m}^2$ , and the maximum luminance of the display was 67  $\text{cd}/\text{m}^2$  (luminance table shown in Supplementary Table 1). The contrast of the Gabor used in the training experiment was 12%, which was determined beforehand by a pilot experiment so that most subjects performed at chance-level when attempting to discriminate the orientation of this stimulus. We have found in previous studies that choosing a

single chance-level signal value from the subject-average psychometric function is more reliable than choosing a different value for each subject based on individuals' psychometric functions, which can be highly unreliable especially at the tails (Seitz and Watanabe unpublished observations). The background noise was redrawn every 300 ms and the onsets and offsets of Gabors were always synchronized to the onsets of the background. In the test sessions, the contrast values of the Gabor were chosen from the set (0%, 15%, 30%, 45%, and 60%), with the contrast-range of the background set to 100%.

## Procedure

The experiment consisted of ten sessions; first a practice session to acquaint subjects with the Gabor sensitivity task, second a pre-test, then seven training sessions, and finally a post-test (Figure 1b). Each session was conducted on a separate day.

### *Pre-/post-test sessions*

Sensitivity to the Gabor stimuli was measured before and after the training phase for each subject using the method of constant stimuli. In each trial, a Gabor pattern was presented at one of the two locations (see schematic in Figure 2) for 300 ms, followed by a ring of lines indicating the three possible orientations of the Gabor. The orientations were 15, 75, and 135 deg clockwise relative to the vertical line when presented in the right visual field, and mirrored orientations (-15, -75, and -135 deg) in the left visual field. They were centered at 3.0 deg apart from the fixation. The task consisted of a three alternative forced choice (3AFC) and the subject responded by pressing a key corresponding to the perceived orientation. Each of the 3 orientations was presented equally often at the 5 contrast levels (including 0% contrast) and with the two spatial frequencies. Each of these 30 conditions was repeated 3 times in each block. A session consisted of 12 blocks of 90 trials, 1080 trials in total. Different Gabor contrasts were interleaved and locations of the Gabor were blocked. Six blocks were used for each location and block order was randomized.

### *Training sessions*

In the training sessions, subjects were asked to perform a peripheral rapid serial visual presentation (RSVP) character identification task while maintaining fixation on a dot presented at the center of the screen. Spatial configuration of the experiment is shown in Figure 2. Two RSVP sequences were presented, one at left and one at the right side of the visual field. Subjects were directed to attend to one of the sequences and report target characters of that sequence. The side of the task was randomly chosen for each subject and instructed beforehand. For each subject, the side of the task did not change through the entire training and the

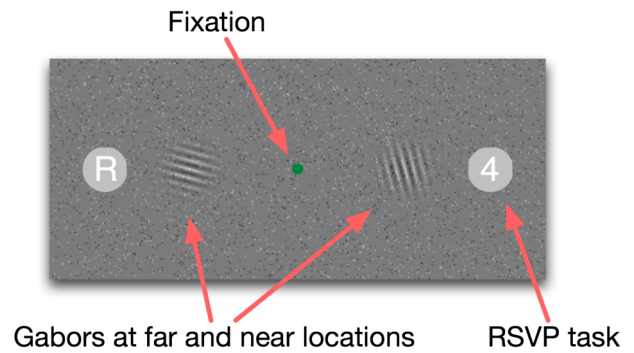


Figure 2. Schematic figure for spatial configuration of visual stimuli used in Experiment 1. The contrasts of the Gabors were subthreshold in the actual experiment. The side of task is balanced across subjects.

subjects could ignore the unattended character sequence. The centers of the circles around the RSVP sequences were located at 5.0 deg apart from the fixation point. Thus, the distances from near and far Gabors to the task RSVP were 2.0 and 8.0 deg, respectively.

In each trial, the attended RSVP sequence consisted of two digits as the targets and nine alphabets as the distractors. At the end of each trial, subjects reported with key-presses the identity of the two digits in order of presentation. No feedback was given; as is typical in studies of TIPL (Watanabe, Náñez, & Sasaki, 2001; Seitz & Watanabe, 2003). Potential confusion between characters (like 1 and I) was avoided by removing such alphabets from the set of possible distractors. Each character in a sequence was presented for 100 ms and the interval between consecutive characters was 200 ms. The positions of the target digits in a sequence were randomized for each trial with the constraint that the two targets could not appear consecutively. Only the attended sequence contained digits, and the unattended dummy sequence consisted of only alphabets.

Gabor patches were presented in the subthreshold contrast at two spatial locations, which were positioned between the central fixation and two RSVP sequences. During each trial, the two Gabor orientations, paired-with-target and paired-with-distractor orientations, were presented. One of the two orientations was temporally paired with the two target digits and the other was paired with two of the distractors. Temporal positions of the target and the distractor that are paired with Gabors were randomly, and independently, assigned for each trial (temporal distribution of the Gabors relative to the target digits are shown in Supplementary Figure 5). For each subject, and at each location, the orientation paired with target digits and that paired with distractor alphabets were fixed. One of the three orientations at each location was treated as a control and not presented in the training sessions. The duration of Gabors was 300 ms, and they were presented 100 ms before the onset of paired letters. Thus, the paired letters were presented temporally at the very center of the duration of Gabors. The training session consisted of 400 trials and lasted about one hour.

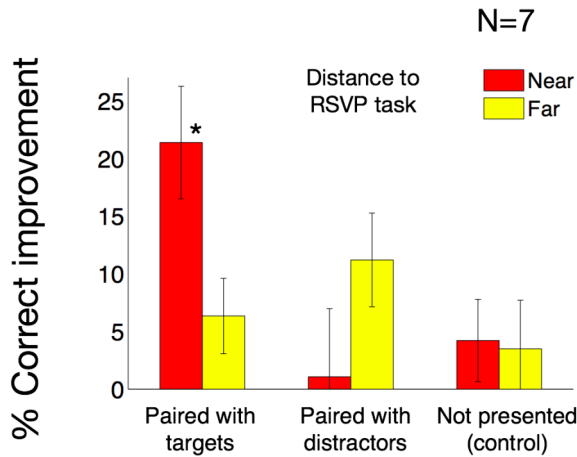


Figure 3. Experiment 1, results. Improvement for each location and orientation is shown. Error bars are the standard error of the mean (SEM). Single star shows significance of a post hoc test (Tukey's HSD,  $p < .05$ ). Significant improvement was found for the Gabor that was shown at spatially closer to the task and temporally paired with the target characters.

## Results

For the RSVP training task, performance significantly improved were found across sessions (one-way ANOVA,  $F(6,6)=20.5$ ,  $p < .001$ ). Mean percent correct was  $61\% \pm 7.1\%$  (standard error of the mean, SEM, across subjects) for the first session, and  $83\% \pm 3.3\%$  for the last session (see Supplementary Figure 1).

To evaluate changes in Gabor sensitivity, each subject's performance was evaluated before and after training on six oriented Gabor stimuli (three at each of the two locations). We expected the transfer of learning effects between the two paired-Gabors to be minimal due to the fact that they differed both in location and in orientation. In this way, we could separately examine possible learning effects for the Gabors paired at the near vs. far locations as well as those paired with the target vs. distractor characters.

The performance change was calculated as the summed difference in performance across contrast levels between the pre- and post-tests. Figure 3 shows the result for each spatial location and pairing condition (raw psychometric functions are plotted in Supplementary Figure 2). A two-way repeated measures ANOVA (distance  $\times$  orientation) revealed significant effect of orientation ( $F(2,12)=7.33$ ,  $p < .01$ ) and significant interaction of distance and orientation ( $F(2,12)=5.765$ ,  $p < .02$ ). A post hoc analysis (Tukey's HSD,  $p < .05$ ) showed significantly higher improvement for the paired-with-target Gabor presented near the task location.

In order to control for the possibility that these results are due to a spatial bias in eye-movements towards the task-relevant RSVP sequence, we measured the eye movements of two of the subjects in Experiment 1 during the

training sessions. We found that the subjects were extremely good at fixating their eyes to the central dot while performing the task. We did not find any significant spatial bias of eye movements that correlated with the presentation of the task targets. Given that we examined eye movements in only in a few sessions, we cannot entirely rule out a possible involvement of eye movements in the spatial restriction of TIPL, but we find these to be an unlikely explanation of our results.

## Discussion

We found TIPL for the orientation of the static Gabor patterns paired with targets of the subject's RSVP task. These results replicate previous findings of TIPL, where the performance on a task-irrelevant feature improves even without the subject's knowing the presentation of the feature. Importantly, we have shown for the first time that TIPL occurs not only for the motion-direction stimuli that have been used in earlier studies, but also for static-orientation stimuli. These two types of stimuli (orientation and motion) are believed to be processed predominantly in different visual processing streams, and our results suggest that TIPL is a general learning property of the visual system.

We also observed a larger learning effect for the Gabor stimuli presented closer to the task location. These results indicate that the learning signal has a spatially limited effect on irrelevant visual inputs. A number of factors make us confident that this spatial restriction of TIPL is not due to trivial effects of stimulus configuration, or eye position. First, as stated in the results, no positional bias in eye-movements, either towards or away from the task-targets, was observed in the subjects for whom eye movements were monitored. Second, the spatial configuration of visual stimuli is horizontally symmetrical and thus we minimized asymmetries in stimulus interactions or a spatial bias caused by exogenous attentional effects. Third, the Gabors were presented as subthreshold (and subjects were required to direct focused attention to the location of the RSVP task). Thus, we are thus confident that subjects did not know that visual Gabor patterns were presented during the training sessions. Altogether, these factors indicate that the spatial restriction of learning is likely due to either spatial effects of endogenous attention and/or spatial effects of the hypothesized learning signal.

The results of the present experiment show the learning signal has spatially limited effect on the irrelevant visual inputs. However, as only two locations were examined, the detail of the spatial extent of such learning signal is still unclear. Also, because the tested locations spanned both visual hemifields, the results do not disassociate whether the obtained specificity is indicative of a relatively small spatial restriction of learning around the task location, or a more global effect that covers the whole hemifield. To address this question, we conducted Experiment 2, where effects of



TIPL were compared for three locations within a single hemifield.

## Experiment 2

In Experiment 2, we further investigated the spatial specificity using a unilateral configuration of visual stimuli, where the two letter sequences were presented in the upper and lower quadrants of the same visual hemifield, and

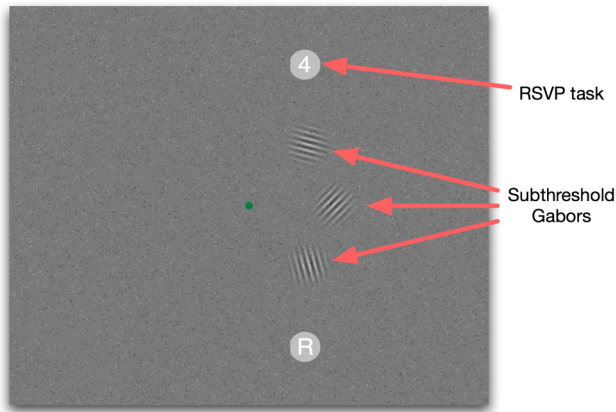


Figure 4. Schematic figure for spatial configuration of the visual stimuli used in Experiment 2. In the actual experiment, the background was filled with random pixel noise (see methods for details). In this example, the locations of the two letter sequences and three subthreshold Gabors are on the right side, and the task is at the upper location. Those conditions are balanced among subjects.

task-irrelevant stimuli were presented at three different, equally eccentric, locations between the letter sequences (Figure 4). The stimuli were arranged so that their spatial locations were spatially symmetrical about the horizontal axis.

## Participants

Nine subjects (6 female and 3 male, age range 18-35 years) who were naïve as to the purpose of the study participated and received payment for their completion of the experiment. All subjects had normal or corrected-to-normal vision.

## Apparatus

We used the same experimental apparatus as those used in Experiment 1, with the exception that the monitor was a ViewSonic VX922 19" LCD with resolution of 1280 x 1024 pixels and minimum response time of 2 ms. The monitor was adjusted so that the luminance range was qualitatively matched to that of the CRT monitor used in Experiment 1. Given that a number of parameters have changed between Experiments 1 and 2, only a qualitative comparison of results across the experiments is valid. Our main purpose in

determining monitor settings is to achieve reliable psychometric functions in the experiments.

## Procedure

The experiment consisted of ten sessions; first a practice session to acquaint subjects with the Gabor sensitivity task, second a pre-test, then seven training sessions, and finally a post-test (Figure 1b). Each session was completed on a separate day.

## Stimuli

Gabors were presented at one of the three possible locations that were centered 3.0 deg apart from the fixation (see Figure 4). The middle location was horizontally aligned to the fixation, and the other two were at the locations  $\pm 45$

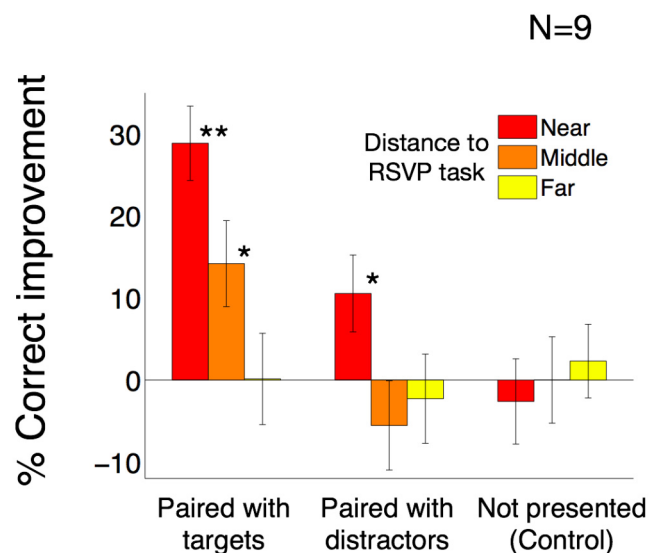


Figure 5. The result of Experiment 2. Improvement for each location and orientation is shown. Error bars are the standard error of the means (SEM). Double stars shows the improvement was significantly higher than each of the other conditions. Single stars show their improvement was higher than each of the no star conditions (Tukey's HSD,  $p < .05$ ).

deg rotated around the fixation. The orientations used in this experiment were the same (15, 75, and 135 for the right side and -15, -75, and -135 for the left side) as those used in Experiment 1. The sigma of the Gaussian factor of the Gabor was 0.6 deg. Gabor pattern and background random dots were mixed so that 70% of pixels were the background noise and 30% was Gabor. In this experiment, 30% of the noise pixels were chosen to be the intermediate gray value so as to avoid textural cues at 0% contrast. We used a slightly different signal-to-noise ratio than those in Experiment 1 because the ratio of the Gabor signal to the background noise used in Experiment 1 was too low for some subjects under the configuration of stimuli used in this experiment. The new parameters were determined based on a pilot ex-

periment consisting only of a test-session. The mean background luminance was 42 cd/m<sup>2</sup>, and the maximum luminance was 83 cd/m<sup>2</sup> (luminance table shown in Supplementary Table 2).

### **Pre-/post-test sessions**

In Experiment 2, we used a 2-interval forced-choice (2IFC) detection task to measure sensitivity at each of the three locations and orientations of presentations via the method of constant stimuli. A trial consisted of two consecutive stimulus presentations (300ms each) with a delay interval (300ms) between them. In each trial, a Gabor pattern was presented at one of the three locations in either the 1st or 2nd presentation interval. The contrast values of the Gabor were chosen from the set (15%, 30%, 45%, 60%, 75% contrast) for the signal interval and 0% for the noise interval. The contrast-range of the background noise was set to 100%. Subjects were instructed to report the interval of Gabor presentation via a keyboard response. A session consisted of 1080 trials in total and lasted about an hour.

### **Training sessions**

The procedure of the training sessions was identical to that of Experiment 1 with the exception that the spatial configuration of the task-relevant and task-irrelevant stimuli (Figure 4). At each location, one of the Gabor orientations was paired with target digits. Another orientation was paired with distractor letters. The third orientation was control and not presented during the training sessions. The contrast of the Gabor presented in the training sessions was 15%, which was determined by a pilot experiment, so that most of the subjects showed chance level performance. The mean performance for 15% contrast in the actual pre-test was 53%  $\pm$  1.8% (SEM across subjects). Thus performance at the exposed contrast level was approximately at chance, and it was unlikely that subjects could have seen Gabor at this level while paying intensive attention to the RSVP task (subject debriefing confirmed that the Gabors went undetected during training). The centers of two letter sequences were 2.0 deg horizontally and 4.5 deg vertically apart from the fixation. The distances of near, middle, and far Gabors from the RSVP task were 2.4, 4.6, and 6.6 deg, respectively.

## **Results**

Significant improvement was observed for the training task (one-way ANOVA,  $F(6,8)=6.8$ ,  $p<.01$ ). Mean percent correct was 27%  $\pm$  8.5% (SEM across subjects) for the first session, and 68%  $\pm$  8.1% for the last session (see Supplementary Figure 3).

The changes in sensitivity between the two test sessions for the task-irrelevant Gabors are shown in Figure 5. A two-way repeated measures ANOVA (distance  $\times$  orientation) revealed significant effect for both distance ( $F(2,16)=4.502$ ,  $p<.05$ ) and orientation ( $F(2,16)=6.250$ ,  $p<.01$ ). The interaction of distance and orientation was also significant ( $F(4,32)=5.720$ ,  $p<.002$ ). A post hoc analysis (Tukey's HSD,  $p<.05$ ) was conducted for further analysis, and it showed

significantly high improvement for paired-with-target Gabors presented at either near or middle location. It was also shown that the improvement at the near location was significantly higher than that at the middle location. In summary, the improvement was highly significant for the Gabors presented at closest location to the task, and also significant at the intermediate location. Importantly, the improvement at the intermediate location was significantly smaller than the closest location.

The post hoc test also showed a significantly higher improvement in paired-with-distractor condition, when the Gabor was presented closest to the target (Tukey's HSD,  $p<0.05$ ), this latter effect may be evidence of the temporal profile of TIPL (see discussion).

## **Discussion**

The results of Experiment 2 confirm those of Experiment 1 showing a spatial restriction of TIPL. In Experiment 2, we further find evidence that the magnitude of learning may fall off smoothly with distance from the locus of the task.

An additional result was that significant improvement found for the orientation that was paired-with-distractors in the location closest to the task-locus. We suggest that this result may provide an indication of the temporal profile of learning. Namely, that learning may be explained by the fact that target letters appeared temporally close to the Gabors paired with distractor letters. In this experiment, the Gabors paired with distractors were presented just before the onset of the target letter with about .2 probability, and also just after the offset of the target letter with about .2 probability (see Supplementary Figure 5 for histograms of temporal offsets between target-characters and distractor-Gabors). In those cases, the inter-stimulus interval between the target-character and the Gabor paired with the distractor-character is only 100ms. Thus learning of the orientation paired with distractors may be explained by a relatively broad temporal profile of the learning signal. However, while this explanation is sensible we are cautious regarding the validity of the learning for the distractor Gabor given that a similar effect was not observed in the equivalent condition of Experiment 1 nor in previous studies of TIPL. The effect here is smaller than that found for the paired-with-target Gabors and is unclear whether it is a false positive or whether it is due to methodological differences between this and other experiments. More detailed examination is required to clarify this point and to explore the temporal characteristics of TIPL.

## **General discussion**

In this study, we investigated how TIPL depends on the relative spatial locations of task-relevant and task-irrelevant stimuli. In both Experiments 1 and 2, we used a RSVP letter detection task, which required the subjects to maintain intensive attention on the location of task-relevant stimuli.

Our results provide evidence that the effects of TIPL fall off as a function of the distance between the task-relevant target and task-irrelevant stimuli. The results also show for the first time that the TIPL occurs for stimulus features other than motion directions in a configuration in which attention is strictly controlled. Namely, we found TIPL effects on the orientation of the static Gabor patterns to which subjects were exposed.

A key finding in this study is that TIPL was most robust for the Gabor presented closest to the locus of the attended task and fell off gradually from that point. Sensitivity to the Gabors was significantly more enhanced when they were presented in the same visual hemifield as the task in Experiment 1. In Experiment 2, three different locations in the same visual hemifield as the task were examined, and we found that learning was the greatest when the learned visual feature was presented closest to the task, and that the amount of enhancement gradually decreased at more distant locations.

It is noteworthy that unlike our previous studies showing TIPL on motion, a significant performance enhancement was found for the Gabor orientation paired with distractor characters, when it was presented at the location closest to the task. However, the enhancement was weaker than that found for the Gabor orientations paired with target characters. This result is in line with our hypothesis that temporal relationship between task targets and task-irrelevant features is important. A possibility is that temporal window of the learning signal induced by the successful detection of targets is so broad that the signal may affect the Gabors presented temporally close to the target characters (see Supplementary Figure 5 for histograms of temporal offsets between target-characters and distractor-Gabors). This interpretation seems plausible but does not simply explain why we did not find the similar effect in the Experiment 1. Therefore until replicated we remain cautious regarding the validity of the learning effect found in paired-with-distractor condition. Further investigation will be required to more clearly specify the temporal profile of TIPL.

Previous studies of TIPL have demonstrated that learning can occur for subliminally presented stimuli. This also seems to be true in the present studies. While it is difficult to prove that the Gabor stimuli were at all times truly subliminal, we have some confidence that subjects did not perceive the Gabors while performing the RSVP task. The subjects were required to direct intense attention towards the task-relevant stimuli and this made it difficult to attend to the location of the task-irrelevant stimuli. In addition, in the testing sessions of Experiment 2, when the Gabors were task-relevant stimuli and attention was directed to them, subjects were unable to detect the Gabor stimuli at the contrast level presented during the RSVP task (mean performance  $53\% \pm 1.8\%$  SEM). Furthermore, no subject reported noticing that the Gabor patterns were presented during the training sessions.

One might ask why TIPL is typically observed when using subthreshold stimuli. One explanation is that this is a result of the fact that TIPL is typically studied as an attempt to show that learning can occur in the absence of awareness (Seitz & Watanabe, 2005). However, other studies have found that task-irrelevant stimuli are not always learned (Ahissar & Hochstein, 1993; Shiu & Pashler, 1992; Polley, Steinberg, & Merzenich, 2006). We have previously argued that other studies did not manipulate the correlation between the task-relevant and task-irrelevant stimuli and that these studies typically resemble our paired-with-distractor condition, which usually shows no learning. However, a recent study showed that activity in visual area MT+ showed peak activation to perithreshold task-irrelevant motion signals in the context of a RSVP task as compared to suprathreshold task-irrelevant stimuli. This result presents the possibility that TIPL is most significant when subthreshold stimuli are used (Tsushima, Sasaki, & Watanabe, 2006).

Provided that perithreshold stimuli are used, the results of this and other studies of task-irrelevant learning support the hypothesis that TIPL is not highly sensitive to the parameters of the stimuli. Studies of TIPL using motion-stimuli have found similar learning effects for motion coherence algorithms using fixed-speed noise (Watanabe, Náñez, & Sasaki, 2001; Seitz & Watanabe, 2003) or white noise (Seitz, Lefebvre, Watanabe, & Jolicoeur, 2005) as well as 100% coherent, but low contrast moving-dots (Seitz, Náñez, Holloway, Koyama, & Watanabe, 2005). The current study adds to this by showing that TIPL works for static orientation stimuli and is qualitatively similar under the different contrasts, signal-to-noise ratios and monitor characteristics (CRT vs. LCD). While altogether this still represents a limited range of stimulus conditions, our collected results show that different strategies of degrading the perception of the task-irrelevant stimuli can be used to achieve TIPL. Further research will be required to explore the relationship between the saliency of the task-irrelevant stimuli, effects of stimulus parameters, and the degree and quality of subsequent learning.

What is the underlying mechanism that leads to a spatially limited profile for TIPL? One possible interpretation is that TIPL results from a learning signal that has a spatially limited extent. Seitz and Watanabe (Seitz & Watanabe, 2005) proposed a model to explain both task-irrelevant and task-relevant learning in which task-related signals (either due to external or internal factors) serve to reinforce activity in low-level sensory processing stages in a stimulus non-specific manner. A possible brain mechanism could be related to some neuromodulators released by successful performance of the task modulating PL. While these learning signals have previously been considered to have broader spatial extent, the present results may provide evidence that these learning signals may be more focused than previously thought.

Another possibility is that the learning signal itself is broad but another process, such as attention, interacts with

this to produce a spatial restriction of learning. For instance, attention may operate to enhance activity to stimuli presented in proximity of the task-relevant stimuli, or suppress activity related to more distal stimuli. Such a possibility seems likely given that attention is well known to evoke spatially restricted effects (Eriksen & St James, 1986; LaBerge, Carlson, Williams, & Bunney, 1997; Muller, Mollenhauer, Rosler, & Kleinschmidt, 2005; Posner, 1980). In addition, while TIPL is characterized by the fact that it does not require the learners to recognize the learned visual feature, it has been suggested that attention toward an accompanying task serves to regulate PL (Seitz & Watanabe, 2005).

We showed the TIPL occurs for static Gabor stimuli. However, we cannot rule out the possibility that some aspects of the underlying mechanisms for the current results are different from the TIPL on motion. Perception of Gabors and characters both involve processing of oriented line segments, while random-dot motion perception does not. The interaction between the letter task and learning of Gabors found in the present study could be a result of attentional modulation to such featural processing. If that is the case, testing spatial extent using motion stimuli could show a different result.

A natural question in evaluating these data is which aspects can be attributed to attentional processes and which are related to reinforcement learning signals? We have suggested previously that these potentially disparate accounts of TIPL via attentional or reinforcement-learning signals may be reconciled by the observation that attention is not a singular process, but instead consists of multiple systems that have different spatial and temporal profiles (Seitz & Watanabe, 2005). For instance, research of Posner and colleagues suggest that alerting, orienting and executive function are triply dissociable attentional subsystems (Posner & Petersen, 1990; Fan, McCandliss, Sommer, Raz, & Posner, 2002). The alerting system controls a non-specific arousal state, the orienting system directs resources to a specific spatial cue or feature, and the executive system is involved in solving a task involving conflict. The orienting and executive systems are suggested to selective to regions of space (spatial attention), individual features (feature-based attention) or objects (object-based attention) regarded to be task-relevant items. Whereas, alerting is a temporally phasic but featurally nonspecific signal that increases general processing at times important stimuli are thought to be present (temporal attention). Interestingly, each of these attention subsystems has been linked with different neuromodulatory signals (Fan, McCandliss, Sommer, Raz, & Posner, 2002); orienting with the acetylcholine system (Davidson & Marrocco, 2000), alerting with the norepinephrine system (Coull, Frith, Frackowiak, & Grasby, 1996; Marrocco, Witte, & Davidson, 1994; Witte, Davidson, & Marrocco, 1997) and executive with dopamine (Fossella et

al., 2002). Importantly, acetylcholine, norepinephrine, and dopamine are known to be involved in learning (Dalley et al., 2001; Schultz, 2000) and have been proposed to have distinct roles in reinforcement learning (Dayan & Balleine, 2002; Dayan & Yu, 2003; Doya, 2002). These findings suggest that attention and reinforcement-learning signals may be subserved by the same substrate. If this is indeed the case, then the important question in evaluating the present set of results is not whether attention or reinforcement-learning signals are responsible for the restricted spatial-temporal profile of learning, but rather which attentional/reinforcement signals are responsible and how do they interact in shaping TIPL?

Our results, combined with the previous findings, indicate that task-irrelevant visual learning is spatiotemporally regulated by brain activity related to successful detection of task targets. It is not clear what brain mechanisms underlie this connection between task and task-irrelevant learning. To clarify this, it is important to measure the spatial profile of the signals mediating TIPL. Our results showed that there is a clear spatial gradient of the learning although more extensive investigation is necessary to clarify the overall shape of this learning function. Further work will be required to specify which attentional/reinforcement systems are involved in TIPL and how their spatial and temporal profiles interact to produce learning.

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## Supplementary Figures

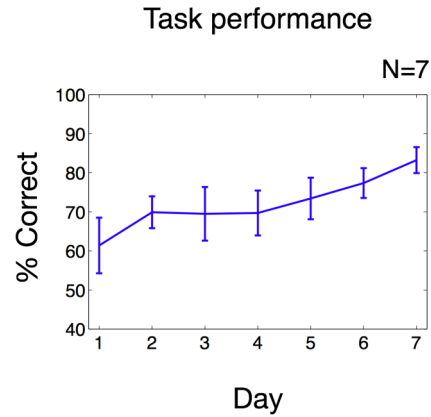


Figure S1. Performance on RSVP task in Experiment 1. Error bars are standard error of the mean (SEM).

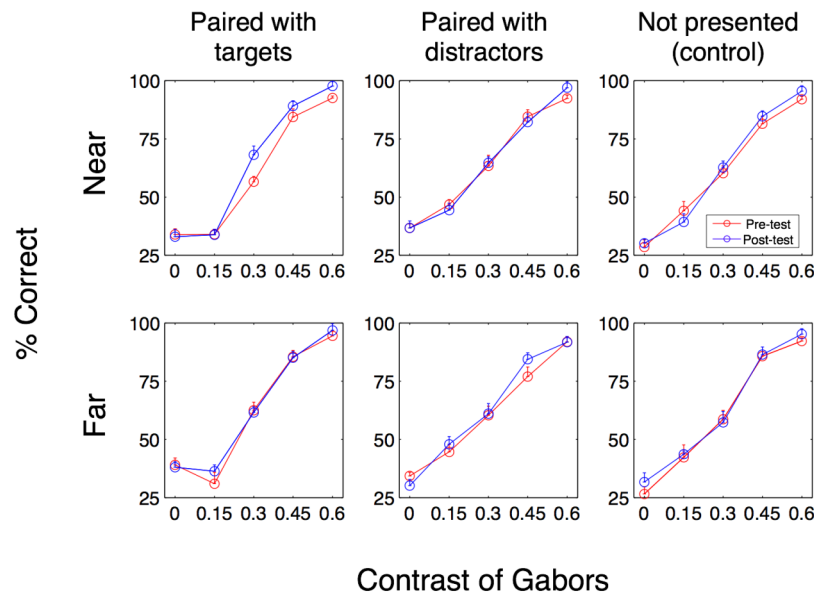


Figure S2. Psychometric functions obtained from the test sessions are plotted for each spatial location and pairing condition. The red and blue lines are pre- and post-test results, respectively. The detectability was almost chance (33%) at the weakest contrast and monotonically increased for the higher contrast. It is important to note that for the 0% contrast trials there is no correct answer. Thus, instead of calculating a value of performance, the bias was established by counting the number of choices made of each orientation, and dividing this by the total number of trials (for that contrast at that location) (Seitz, Náñez, Holloway, Koyama, & Watanabe, 2005). Each value for 0% contrast thus represents a bias, not an actual percent-correct value. Error bars are standard error of the mean (SEM).

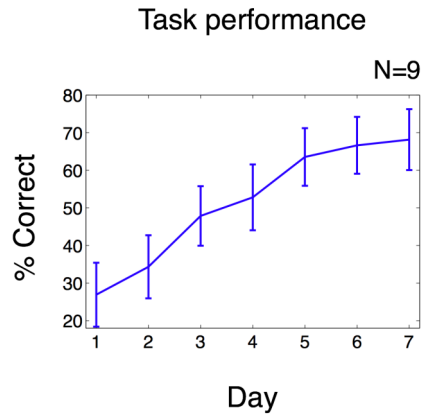


Figure S3. Performance on RSVP task in Experiment 2. Error bars are standard error of the mean (SEM).

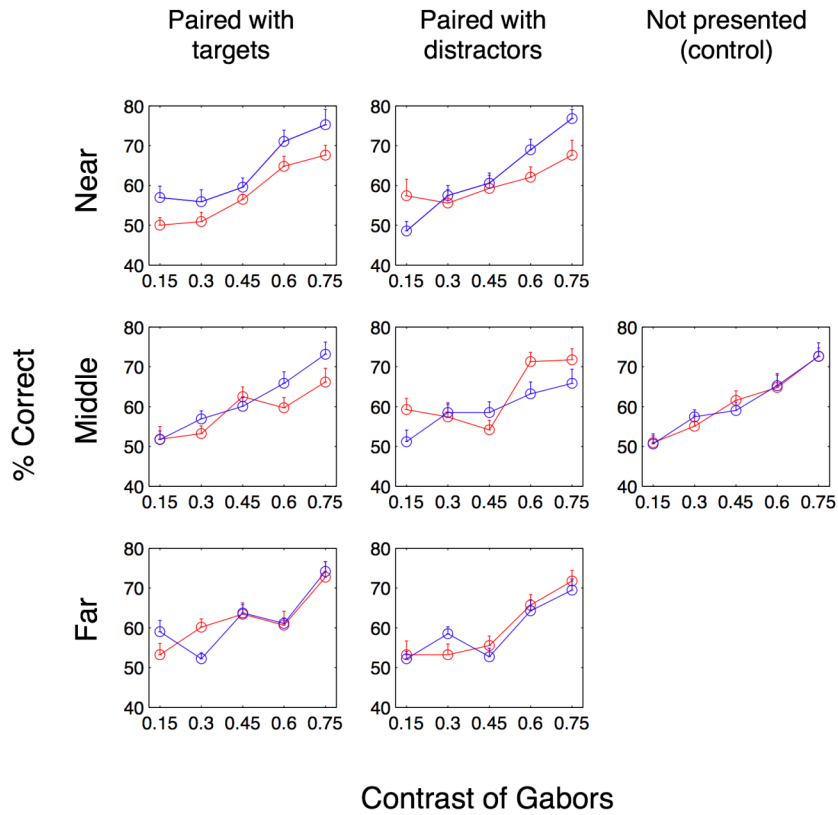


Figure S4. Psychometric functions obtained from the test sessions are plotted for each spatial location and pairing condition. The detectability was almost chance (50%) at the weakest contrast and monotonically increased for the higher contrast. The red and blue lines show the results of pre- and post- tests respectively. Error bars are standard error of the mean (SEM).



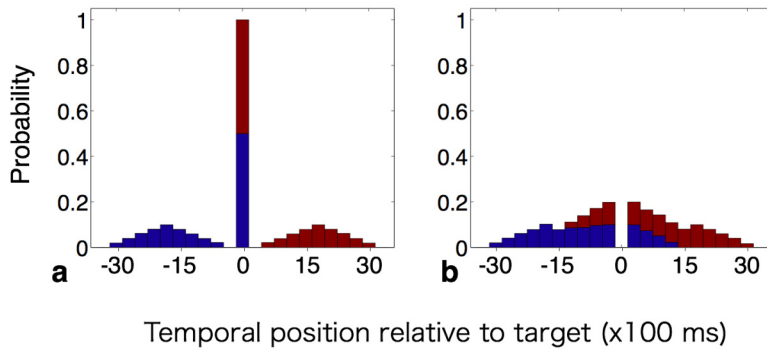


Figure S5. Probability of paired-with-target Gabors (a) and paired-with-distractor Gabors (b) appearing at times relative to target digits. Two set of probabilities that are based on the first and the second targets are shown in different colors (red is based on the first target and blue is on the second). The x-axes show relative temporal positions. See Procedure section of Experiment 1 for detail about the presentation timing of Gabors and characters.

## Supplementary Tables

Table S1. The relationship between gray level values and actual luminance shown on the CRT monitor used in Experiment 1.

Gray level (0 to 255)	0	32	64	96	128	160	192	224	255
Luminance (cd/m <sup>2</sup> )	1.59	7.99	15.13	23.48	33.27	45.87	55.21	63.32	66.88

Table S2. The relationship between gray level values and actual luminance shown on the LCD monitor used in Experiment 2.

Gray level (0 to 255)	0	32	64	96	128	160	192	224	255
Luminance (cd/m <sup>2</sup> )	15.03	18.81	24.22	32.75	42.04	52.74	63.66	74.33	83.14