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Interference and feature specificity in visual perceptual learning

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A B S T R A C T

Perceptual learning (PL) often shows specificity to a trained feature. We investigated whether feature specificity is related to disruption in PL using the texture discrimination task (TDT), which shows learning specificity to background element but not to target element. Learning was disrupted when orientations of background elements were changed in two successive training sessions (interference) but not in a random order from trial to trial (roving). The presentation of target elements seemed to have reversed effect; learning occurred in two-parts training but not with roving. These results suggest that interference in TDT is feature specific while disruption by roving is not.

1. Introduction

It was once thought that after a critical period of one's early life the brain becomes rigid, allowing little plasticity in the adult brain (Hubel & Wiesel, 1965). However, recently, a large number of studies have shown that adults repeatedly exposed to or trained on a visual feature exhibit improved performance on that feature (Fahle & Poggio, 2002). Such experience-dependent performance enhancement is called *perceptual learning (PL)*. To date, the mechanism underlying PL has not been clarified, but psychophysical investigations of PL have provided insights into the nature of cortical plasticity in the adult brain.

One of the characteristics of visual PL is specificity to features of a trained stimulus (Fahle, 1997); learning of trained features does not often transfer to features that were not trained. The specificity of PL has been found for a variety of stimulus features such as motion direction (Ball & Sekuler, 1982, 1987; Saffell & Matthews, 2003; Vaina, Belliveau, des Roziers, & Zeffiro, 1998; Watanabe et al., 2002), orientation (Yu, Klein, & Levi, 2004), spatial frequency (Fahle, 1994; Fiorentini & Berardi, 1980; Poggio, Fahle, & Edelman, 1992; Sowden, Rose, & Davies, 2002), and location (Sowden et al., 2002). Additionally, it has been shown that the training is specific to an eye to which the trained stimulus is presented during training (Fahle, 1994; Poggio et al., 1992). Such specificity of learning has led a number of researchers to suggest that early-level visual processing is involved in some types of PL (Karni & Sagi, 1991; Poggio et al., 1992; Schoups, Vogels, Qian, & Orban, 2001; Schwartz, Maquet, & Frith, 2002; Yotsumoto & Watanabe, 2008; Yotsumoto; Watanabe, & Sasaki, 2008) (but see Dosher and Lu (1998)).

Clarifying the training conditions by which PL occurs or does not occur is useful for obtaining insights into the possible mechanisms of PL. Many investigators have reported that PL is reduced or blocked by two types of training paradigms: *roving training* (Adini, Wilkonsky, Haspel, Tsodyks, & Sagi, 2004; Kuai, Zhang, Klein, Levi, & Yu, 2005; Mollon & Danilova, 1996; Otto, Herzog, Fahle, & Zhaoping, 2006; Tartaglia, Aberg, & Herzog, 2009; Xiao et al., 2008; Yu et al., 2004; Zhang et al., 2008) and *a two-part training* causing interference (Seitz et al., 2005).

Roving is a training schedule under which multiple stimulus features are randomly interleaved from trial to trial. It has been reported by many that roving training, in which one must discriminate between contrasts, tends to impede or weaken learning compared to training with only a single contrast (Adini et al., 2004; Kuai et al., 2005; Mollon & Danilova, 1996; Otto et al., 2006; Tartaglia et al., 2009; Xiao et al., 2008; Yu et al., 2004; Zhang et al., 2008). Some have argued that the failed or weak PL resulting from roving training is an indicator that roving hinders decision-making (Adini et al., 2004), stimulus predictability (Zhang et al., 2008), or memory tracing, which take place more centrally, as higher-level processes, than in early sensory areas (Kuai et al., 2005; Mollon & Danilova, 1996; Xiao et al., 2008; Yu et al., 2004).

Interference caused by two successive training sessions provides another example of failure or reduction of PL. Interference

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refers to a failure to learn one task (task A), when training is immediately followed by training for a similar but different task (task B), whereas learning of task A does occur when it is practiced alone. Interference also occurs in motor learning. When training of one motor task (A) is followed by training of another motor task (B), learning of A is disrupted by task B or, vice versa, B by A (Brashers-Krug, Shadmehr, & Bizzi, 1996; Krakauer & Shadmehr, 2006; Shadmehr & Brashers-Krug, 1997; Shadmehr & Holcomb, 1997; Walker, Brakefield, Hobson, & Stickgold, 2003). Interference has led researchers to believe that following training for a specific task, learning must be stabilized or consolidated and, if training of another new task occurs during this critical stabilization or consolidation period, PL of the first task is disrupted (interfered). The magnitude of interference becomes smaller as the time interval between training sessions for tasks A and B is increased (Brashers-Krug et al., 1996); as such, the presence of interference is regarded as existence of the critical period for stabilization or consolidation. Seitz et al. (2005) demonstrated that such interference also occurs with PL on vernier acuity tasks (Seitz et al., 2005). When subjects were trained with just one offset-orientation in a three-dot vernier acuity task, their performance improved at the trained visual location with the trained offset-orientation. However, when subjects were trained first with one offset-orientation, and then, immediately afterward, trained with another offset-orientation at the same trained visual location, the second training interfered with PL of the first offset-orientation. Interestingly, interference of learning was not found if trained stimuli in the two training series were presented in different locations, orientations, and offset-orientations (Seitz et al., 2005), which indicates that interference of PL is specific to primitive features and that a low-level stage of visual processing is involved.

In the present study, we address the question of whether and, if so, how PL fails (or is reduced) using the texture discrimination task (or TDT). TDT, a standard task for PL research, has unique characteristics that lend themselves to studies of learning specificity (Karni & Sagi, 1991). In TDT, both a target (foreground) and background are made of textures of short line elements (for example, Fig. 1). A target consists of three line elements, the orientation of which differs from the orientation of the background elements. Interestingly, although a learning effect was observed in a TDT study when subjects were tested with a target element orientation different from the target element orientation they had seen in training, no-learning effect was observed when the orientation of the background texture elements in testing differed from that seen in training (Karni & Sagi, 1991). That is, it seems that TDT learning is specific to the orientation of the background elements of stimulus, and not specific to the orientation of the target elements in the foreground. Thus, a unique characteristic of TDT is that the learning specificity of line orientation depends on whether lines belong to target or background (Karni & Sagi, 1991).

For our study, during training for TDT, we presented different target element orientations and/or background orientations in two different ways: in random order (roving training) or in two successive parts of training (two-part training). We found that roving training with target element or background element interleaved led to PL, although the former learning was slightly weak. In contrast, a two-part training with different background orientation did not lead to PL. However, a two-part training with different target element orientation did lead to PL.

These results suggest important implications of the mechanism for TDT learning and interference. First, the findings that PL occurred in the roving with different background element orientations but not in the two-part training are in accord with the hypothesis that learning of the background element orientation in TDT mainly involves a low-level stage of visual processing, as roving is suggested to impede more central stages (Adini et al., 2004; Kuai et al., 2005; Xiao et al., 2008; Zhang et al., 2008) and interference is suggested to occur in a lower stage (Seitz et al., 2005). Second, the findings that PL occurred both in the two-part training condition and in the roving condition with two different target element orientations (though less strongly), suggest either that learning of target element orientation is not requisite in TDT learning or that learning of target element orientations, mainly involves a higher-stage of visual information processing.

2. General methods

We conducted three experiments. Here we describe methods that were common to all three experiments. In Sections 3–5, following, we individually describe methods specific to each experiment.

2.1. Participants

A total of 36 subjects with normal or corrected-to-normal vision participated in this study (12 subjects in each of the three experiments); 16 of the 36 participants were male, 20 female. The age range was 18–30 years old, with a mean age of 21.3 years. None of the subjects had prior experience in the task used in this study. All subjects gave written informed consent for their participation in the experimental protocol, which was approved by the Institutional Review Board at Boston University.

2.2. Stimuli and procedure

We employed a texture discrimination task (TDT) that is widely used to study visual PL (Karni & Sagi, 1991). In TDT, subjects are asked to respond to the central letter task and to discriminate the orientation of a target array in the peripheral position in a test stimulus. The purpose of the letter task is to ensure subjects' visual fixation on the center of the stimulus. Subjects' performance of the orientation discrimination task tends to improve with practice.

All of the three experiments included two sessions: one session per day, for 2 days. Each session included 546 trials, which altogether lasted approximately 50 min. In each trial, after 1 s of fixation, a test stimulus was briefly presented (13 ms), followed by a blank interval (stimulus-to-mask onset asynchrony, SOA), and a mask stimulus composed of randomly oriented V-shaped patterns (100 ms). Trials in each experiment were blocked, and SOA was constant for trials in a given block. A series of seven different SOAs (180, 160, 140, 120, 100, 80, 60 ms) were used throughout the experiments. While fixating on the center of the blank screen presented after the mask stimulus, subjects were asked to respond twice in each trial, once to identify the letter they saw and once to indicate the orientation (horizontal or vertical) of the target array. Immediate auditory feedback was given only for the fixation letter task, to encourage subjects' fixation. No feedback was given for the orientation task.

A test stimulus consisted of a centrally located letter, either "T" or "L", and a peripherally positioned horizontal or vertical array of three lines (target array) equally oriented on a background of uniformly oriented lines (Fig. 1). Each line segment of the peripheral target array or background was arranged within a 19×19 lattice, which subtended 19° of visual angle. Lines subtended $0.73 \times 0.13°$ of visual angle. The position of each line segment was jittered slightly, by 0–0.2°, from trial to trial. The position of the target array also varied randomly from trial to trial, but was consistently presented within a specific quadrant (in subjects' upper-left or upper-right visual field, randomly chosen) and within a 5–9° visual angle from the center of the display. All line segments were gray (32 cd/m^2) and presented on a black (0.5 cm/m^2) background. This

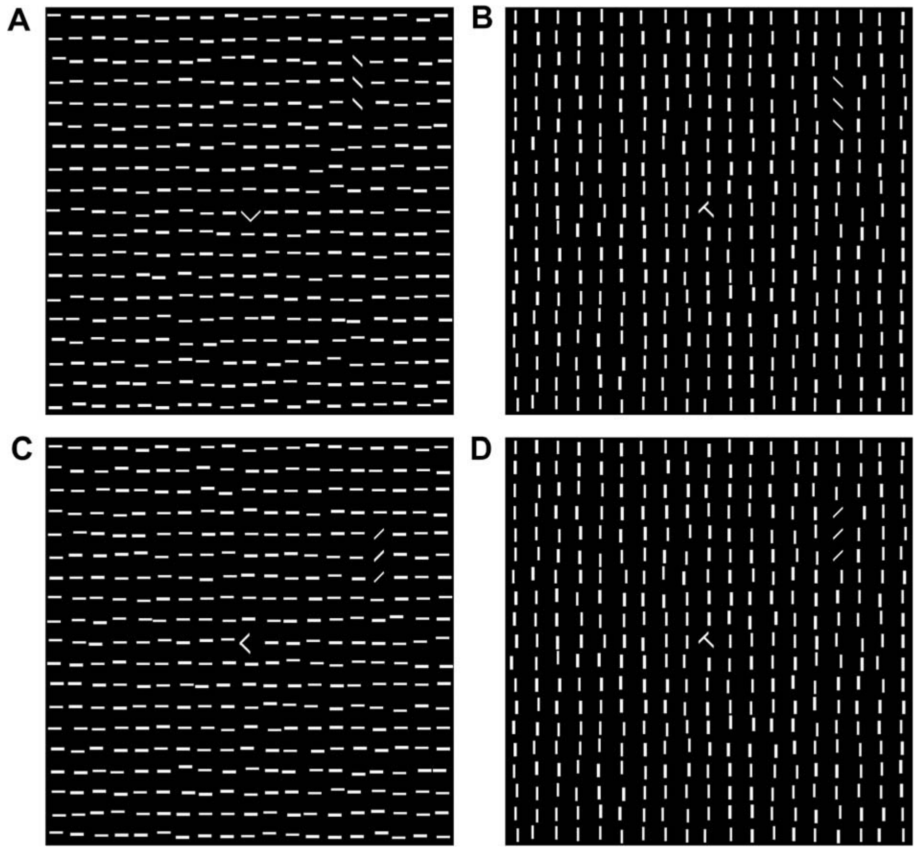

Fig. 1. Examples of test stimuli with a vertical orientation of a target array in the right upper visual field quadrant. In A and B, the target elements orientation is −45° oriented from the vertical, while it is 45° oriented from the vertical in C and D. The background orientation is horizontal in A and C, while it is vertical in B and D. In the Mixed condition, eight combinations of background and target elements orientations were used (see text).

procedure is consistent with the standard procedure of TDT (Karni & Sagi, 1991).

Stimuli were generated by a Macintosh computer, using Matlab six with a psychtoolbox (Pelli, 1997), and presented onto 19 in. CRT monitor. With their chin and forehead fixed, each subject viewed visual displays on a screen positioned 57 cm from their eyes. All experiments were conducted in a dimly lit room.

All subjects took part in two sessions over two consecutive days. In all experiments and for all conditions, the day 2 session was an exact replication of the session on day 1. The correct response rate for orientation discrimination was obtained by individually averaging all trials for each SOA. Individual improvement in correct response rate for each SOA in the TDT, from day 1 to day 2, was used as a measure of PL.

As another measure of performance, we obtained the estimated threshold SOA for each subject. We calculated the percentage of correct responses for each SOA to construct a psychometric function for each subject. Each subject's correct response rate over the SOAs was fitted to a logistic curve. The threshold SOA was defined as the SOA, for which 75% of responses were correct in the interpolated logistic function individually.

3. Experiment 1

3.1. Does TDT learning occur with roving?

In Experiment 1, we examined whether interference in TDT learning occurs by training with multiple combinations of target element and background element orientations interleaved, that is, roving.

For Experiment 1 there were two conditions. One condition (the Fixed condition) employed a conventional texture discrimination task (Censor, Karni, & Sagi, 2006; Karni & Sagi, 1991), where orientations of background elements and target elements were kept constant, or unchanged, throughout all trials. We expected TDT learning to occur in this Fixed condition, as it corresponds to the standard learning set for TDT.

In a second condition (the Mixed condition), multiple background element and target element orientations were presented randomly, trial by trial. The Mixed condition, thus, employs a roving training. If TDT performance involves higher processing including decision-making (Adini et al., 2004) or predictability (Zhang et al., 2008), learning should fail in the Mixed condition. On the other hand, if such higher processing is not involved in TDT performance, we would expect learning to occur in the Mixed condition.

3.2. Methods

Six subjects were assigned to the Fixed condition, and six different subjects were assigned to the Mixed condition.

In the Fixed condition, the orientation of the background elements was always horizontal, and the three target lines were always −45° from the vertical meridian. In the Mixed condition, the background elements were presented in one of four orientations, 90° (horizontal), 0° (vertical), 45° and −45° from the vertical meridian. The orientation of the target elements differed from that of the background elements by either 45° or 135°, so that the relative acute angle between the background elements and target elements was kept constant throughout trials. For example, if the orientation of the background elements was 45° from the vertical meridian, the orientation of the target elements was either horizontal or vertical. In each trial, the orientation of the background elements was randomly selected from these four possible orientations, and the orientation of the target elements was also randomly selected from the two possible orientations. In other words, whereas the Fixed condition contained a single background orientation with a single target element orientation (one combination), the Mixed condition contained four background orientations, each of which was paired with one of two target element orientations, resulting in eight possible combinations of background and target element orientations. It should be noted that subjects' responses to the discrimination task were made in reference to the orientations of target arrays not to the orientations of target elements. The orientation of target arrays was independent from the orientation of the target elements that were manipulated in the Mixed condition.

For both conditions, each session contained 546 trials, which were presented in 21 blocks; the time to complete each session was approximately 50 min. Each of the 21 blocks contained 26 trials with a constant SOA. Each session started with a longer SOA (180 ms), which was decremented by 20 ms every three blocks. Thus, altogether, a series of seven SOAs (180, 160, 140, 120, 100, 80, 60 ms) was used. As the session proceeded, and the SOA in each block was shortened, the difficulty of the task increased.

3.3. Results of Experiment 1

The results of Experiment 1 indicate that PL took place in both the Fixed and Mixed conditions. We calculated the correct response rate for orientation discrimination for each SOA individually; the mean correct response rate, averaged across subjects for each SOA, is plotted in Fig. 2. For the Mixed condition, we averaged all trials with any orientation combination per SOA. Each logistic curve in Fig. 2 is fitted to the mean values for visualization purposes only. Here, the correct response in the discrimination of target arrays was either "vertical" or "horizontal", thus the chance level of correct discrimination for each SOA is 50%, irrespective of the target element orientations. For both the Fixed and Mixed conditions, longer SOA gave better correct response rate. Importantly, the correct response rate improved significantly from day 1 to day 2, indicating occurrence of PL.

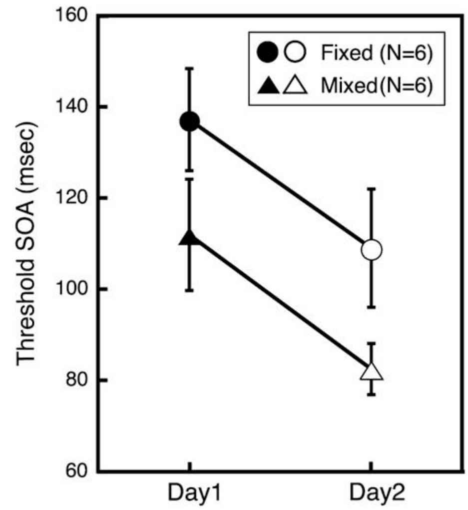

Fig. 3. The mean estimated 75% threshold SOA for the Fixed and Mixed conditions in Experiment 1. Filled symbols are for day 1 and open symbols are for day 2. Error bars represent ±1 standard error of the mean.

In the conventional TDT configuration (the Fixed condition), the results of a repeated measures ANOVA with two within-subject factors (SOA and day) showed a significant main effect for day ($F(1, 5) = 37.04$, $p = .002$) and for SOA ($F(6, 30) = 21.28$, $p < 0.001$). There was no interaction between these factors ($F(6, 30) = 2.113$, $p = .081$).

In the Mixed condition, repeated measures ANOVA with two within-subject factors (SOA and day) also showed a significant main effect for day ($F(1, 5) = 11.607$ $p = .019$) and for SOA ($F(6, 30) = 33.859$, $p < .001$), and with no interaction ($F(6, 30) = 1.606$, $p = .180$).

Next, we estimated each subject's 75% threshold SOA by fitting individually to a logistic curve. The estimated threshold SOA values for day 1 and day 2 averaged across subjects are plotted in Fig. 3. The decrease in threshold SOA values from day 1 to day 2 indicates learning. A repeated measures ANOVA with one within-subjects factor (day) and one between-subjects factor (condition) con-

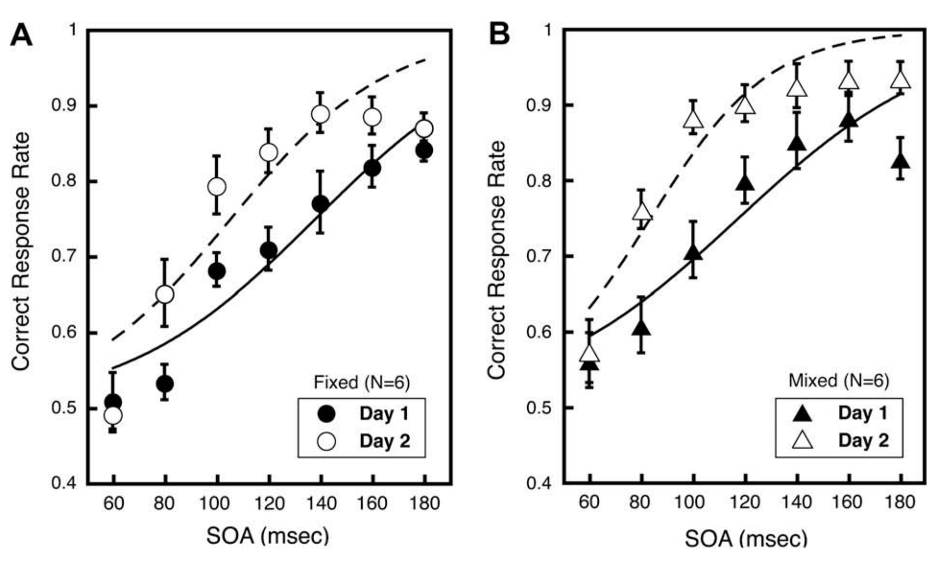

Fig. 2. The mean correct response rate over various SOAs in the Fixed (A) and Mixed (B) conditions. The correct response rate for each SOA was plotted separately for day 1 (filled circles for the Fixed condition and filled triangles for the Mixed condition) and day 2 (open circles for the Fixed condition and open triangles for the Mixed condition). Each logistic curve was fitted to the mean correct response rate across subjects for day 1 and day 2 in each condition just for visualization purpose only. Error bars represent ±1 standard error of the mean.

firmed a significant main effect for day ($F(1, 10) = 30.756$, $p < .001$). There were no significant differences between two conditions ($F(1, 10) = 3.190$, $p = .104$); nor was there significant interaction between condition and day ($F(1, 10) = .016$, $p = .902$).

In addition, we calculated individual decrement of the threshold from day 1 to day 2. In the Fixed condition, the mean threshold decrement averaged across subjects over days is 28.2 ms, which is significantly different from zero (one sample *t*-test, $t(5) = 3.646$, $p = .015$). In the Mixed condition, the average threshold decrement over days is 29.5 ms, which is also significantly different from zero (one sample *t*-test, $t(5) = 4.241$, $p = .008$). Fig. 9 shows the averaged threshold decrement, and Fig. 10, the plot for individual threshold change from day 1 to day 2 for all experiments.

To summarize, the results of Experiment 1 showed that, first, PL took place in both the Fixed and Mixed conditions. Second, the magnitude of PL that took place for both conditions was fairly comparable, as shown in the curves in Fig. 2A and B, or in Figs. 9 and 10. From these results, we concluded that roving training did not result in failed learning in the TDT.

4. Experiment 2

4.1. Interference between different background/target element orientations with two-part training

In Experiment 2, we applied a two-part paradigm to examine whether interference occurs when different background or target element orientations are trained separately, but successively in different parts. As noted above, the results of Experiment 1 showed no failure of learning with roving training. However, in a previous study that reported failure or interference, subjects were trained on two similar but different tasks in separate but successive practice sessions on the same day (Seitz et al., 2005). This finding raises a question as to whether the training schedule affects the occurrence of PL. To address this question, we tested whether PL takes place with a modified training schedule in TDT. We divided 546 trials into two successive parts of training. In the Target condition, the orientation of target elements changed from the first part of the training session (part A) to the second part (part B). In the Background condition, the orientation of the background elements changed from the first (A) to the second (B) part of training.

The question of interest here was whether the presence or absence of interference is paralleled in both Background and Target conditions. Note TDT learning is specific to the orientation of background element but not to the orientation of the target element. If interference is not related to feature specificity, we predicted that the outcome would be the same for both conditions; that is, we would see interference in both Background and Target conditions, or no interference in both Background and Target conditions. By contrast, if interference is somehow related to feature specificity, the presence or absence of interference would not be consistent in both the Background and Target conditions; that is, interference could be present in the Background condition but absent in the Target condition, or absent in the Background condition and present in the Target condition.

4.2. Methods

We randomly divided 12 subjects into two groups, the Background condition and Target condition (six subjects each). In each condition, the training session was subdivided into two successive parts, parts A and B. In the Background condition, two different background orientations were used in training parts A and B. In the Target condition, two different target element orientations were used in parts A and B.

In both the Background condition and Target condition, the total number of trials across the two parts of training was 546. For each of the 2 days of training, the total training session, split into two parts, altogether lasted approximately 50 min. Each part consisted of 273 trials, presented in 14 blocks. Throughout the two parts of training, odd-numbered blocks consisted of 19 trials and even-numbered blocks consisted of 20 trials, such that the total number of trials in Experiment 2 equaled the number in Experiment 1. The SOA was constant for each block. Each session started with a longer SOA (180 ms), which was decremented by 20 ms every two blocks; in all, seven different SOAs (180, 160, 140, 120, 100, 80, 60 ms) were used during each part. After the offset of part A, subjects were forced to take a break for several minutes before starting part B.

In the Background condition, the orientation of target elements was constant throughout sessions, $-45°$ or $45°$ from the vertical meridian, counterbalanced across the subjects. The background orientation was constant within each part (A or B), but differed by $90°$ between parts A and B. Half of the subjects in the Background condition were presented with vertical background elements in part A, and then presented with horizontal background elements in part B. The other half of the subjects in the Background condition were presented with horizontal background elements in part A and vertical background elements in part B. For each subject, parts A and B on day 2 were exact replications of parts A and B on day 1.

In the Target condition, the background orientation was consistently vertical or horizontal for each subject, counterbalanced across subjects. The target element orientation was constant within each part (A or B), but differed by $90°$ between parts A and B. Half of the subjects in the Target condition were presented with a target whose line elements were oriented $45°$ from the vertical meridian in part A and then presented with line elements oriented $-45°$ from the vertical meridian in part B. The other half of the subjects in the Target condition were presented with a target whose line elements were oriented $-45°$ from the vertical meridian in part A and with line elements oriented $45°$ from the vertical meridian in part B. For each subject, Parts A and B on day 2 were exact replications of parts A and B on day 1.

4.3. Results of Experiment 2

We calculated the correct response rate in TDT in the Background condition and Target condition for each SOA in each part of training individually; the mean correct responses, averaged across subjects, for each SOA in each part of the training session is plotted in Fig. 4. The logistic curves shown in Fig. 4 are fitted to the mean values for visualization purposes only. Fig. 4A and B shows performance in part A in both conditions on each day. In the Background condition (Fig. 4A), there was little improvement in the correct response rate from day 1 to day 2 for part A. In part A of the Background condition, the results of a repeated measures ANOVA with two within-subjects factors (SOA and day) showed no significant effect for day ($F(1, 5) = 1.887$, $p = .228$), but significant effect for SOA ($F(6, 30) = 10.888$, $p < .001$). In the Target condition (Fig. 4B), the correct response rate did improve significantly from day 1 to day 2. In part A of the Target condition, the results of a repeated measures ANOVA showed significant main effects for both day ($F(1, 5) = 38.511$, $p = .002$) and SOA ($F(6, 30) = 12.789$, $p < .001$).

Fig. 4C and D shows performance in part B in both conditions on each day. In part B of the Background condition (Fig. 4C), we observed no significant improvement from day 1 to day 2. In part B of the Background condition, a repeated measures ANOVA showed no significant effect for day ($F(1, 5) = .058$, $p = .819$), but significant main effect for SOA ($F(6, 30) = 13.957$, $p < .001$). In the Target con-

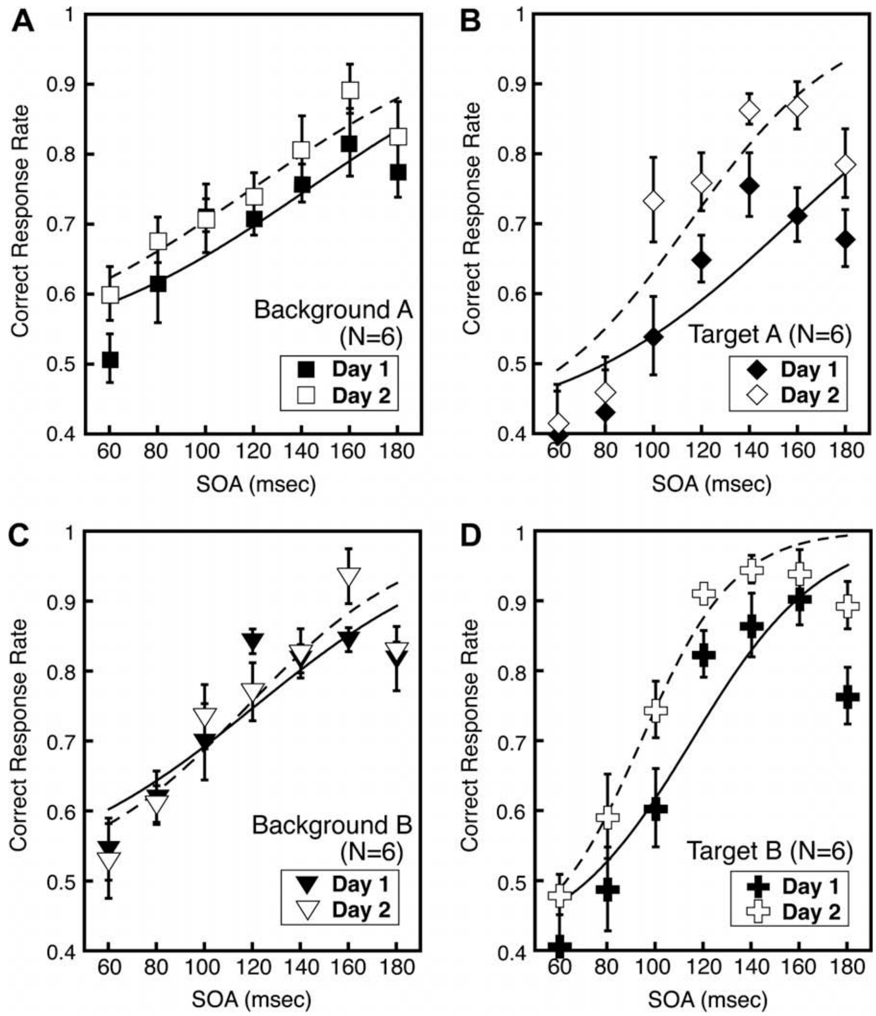

Fig. 4. The mean correct response rate over various SOAs in parts A and B in the Background and Target conditions in Experiment 2. Filled symbols are for day 1 and open symbols are for day 2. Each logistic curve was fitted to the averaged correct response rate across subjects for day 1 and day 2 in each condition just for visualization purpose only. A: Part A in Background condition. B: Part A in Target condition. C: Part B in Background condition. D: Part B in Target condition.

dition (Fig. 4D), however, there was an improvement in the correct response rate from day 1 to day 2 in part B. In part B of the Target condition, repeated measures ANOVA showed significant main effects for both day ($F(1,5) = 29.459$, $p = .003$) and SOA ($F(6,30) = 38.406$, $p < .001$).

We estimated 75% threshold SOA values for day 1 and day 2 individually. Fig. 5 shows the mean thresholds, averaged across subjects; parts A and B in both conditions plotted separately. In the Background condition (Fig. 5A), threshold SOA values did not change from day 1 to day 2, either in part A (paired sample *t*-test, $t(5) = .981$, $p = .372$) or in part B ($t(5) = .030$, $p = .978$). The threshold SOA value in part A in the Target condition did improve from day 1 to day 2 (paired sample *t*-test, $t(5) = 2.598$, $p = .048$), but in the same condition the threshold SOA value in part B did not show improvement across the 2 days ($t(5) = .643$, $p = .549$), perhaps because performance on day 1 was better to begin with – known as a flooring effect. In support of this possibility, the averaged threshold in part B was significantly better than that in part A in the Target condition, even on day 1 (paired *t*-test, $t(5) = 2.54$, $p = .05$).

We additionally analyzed the reaction times (RT) for the orientation tasks to examine whether the lack of learning in the Background condition was due to subjects' fatigue or decreased motivation. If this were the case, RT would increase. Fig. 6 shows the averaged RT for each part (A and B) in each condition for days 1 and 2. Generally, RTs were shorter on day 2 than on day 1 in both the Background and Target conditions, and overall, RTs in the Background condition do not seem to be longer than those in the Target condition. A 3-way ANOVA with one between-subjects (condition) and with two within-subject factors (part and day) showed no significant main effect for condition ($F(1,10) = .357$, $p = .564$), but significant main effects for part ($F(1,10) = 62.748$, $p < .001$) and day ($F(1,10) = 16.174$, $p = .002$). Since the subjects responded to tasks by pressing buttons in a button box in TDT, the general motor component such as key press might be improved in Experiment 2, as the averaged RTs were shorter on day 2 than on day 1 in both parts A and B of both conditions. Importantly, the averaged RT in the Background condition was not statistically longer than in the Target condition.

To summarize the results of Experiment 2, we found no significant PL when two different background element orientations were presented in two successive training parts, with one background orientation per part. The correct response rate for each SOA did not show significant improvement from day 1 to day 2 in either part A or B in the Background condition. The estimated threshold SOA values were also not improved in the Background condition. These data suggest that part B induces interference on part A.

In contrast, PL did occur when two different target element orientations were presented during training in two successive parts.

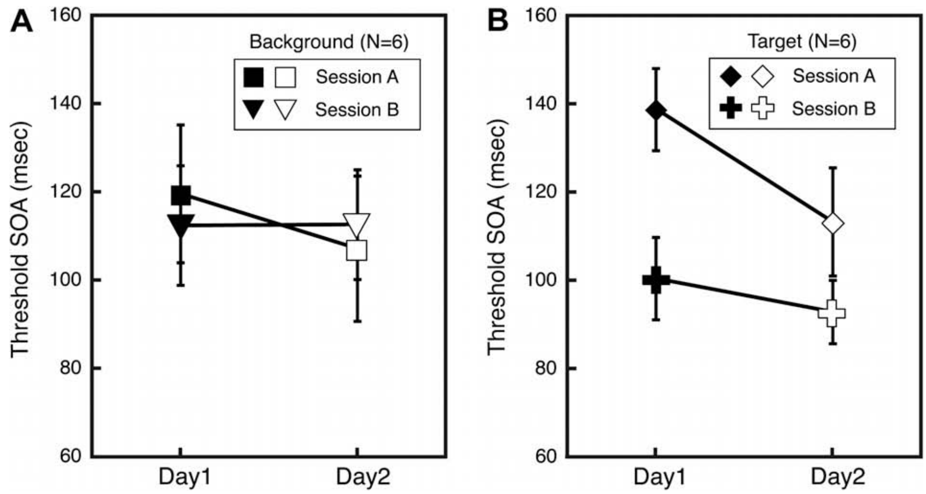

Fig. 5. The mean estimated 75% threshold SOA for Background (A) and Target (B) conditions in Experiment 2. Filled symbols are for day 1 and open symbols are for day 2. Error bars represent ±1 standard error of the mean.

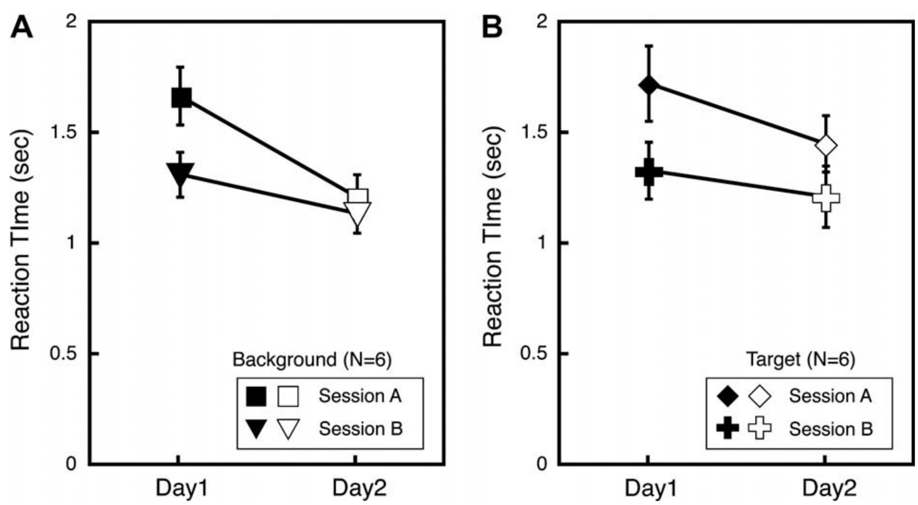

Fig. 6. The mean reaction time (RT) for Background (A) and Target (B) conditions in Experiment 2. Filled symbols are for day 1 and open symbols are for day 2. Error bars represent ±1 standard error of the mean.

The data show that performance in part A was significantly improved from day 1 to day 2 in the Target condition, which suggests that in the Target condition there was no interference on part A caused by part B. Rather, the data suggest that performance improvement was transferred from part A to part B, even on day 1. This finding is in agreement with those in the previous study by Karni and Sagi that showed learning is not specific to the target element orientation (Karni & Sagi, 1991). Moreover, this indicates that only one part of training is sufficient for TDT learning to occur, and that the failure of PL in the Background condition was not due to insufficiencies in the training itself.

The results of Experiment 2 indicate that interference of PL did occur and, in the Background condition, resulted in failure to learn; however, PL did occur in the Target condition. These findings further suggest that interference of PL is somehow related to feature specificity, since PL in TDT is known to be specific to background element orientation, but not to the target element orientation (Karni & Sagi, 1991). If interference has nothing to do with feature specificity, the presence or absence of interference would have been parallel for both conditions.

5. Experiment 3

5.1. Did the number of combination of target–background element orientation matter?

The results of Experiments 1 and 2 together suggest that PL in TDT occurs when training involves random presentation, that is, when training is roving (the Mixed condition in Experiment 1); interference was found to occur only when background element orientation differed when a training session was split into two successive parts (the Background condition in Experiment 2). However, one may wonder whether the above difference is due to the different number of combinations of target–background orientation in experiments. In the Mixed condition in Experiment 1, there were eight possible target–background orientation combinations, while there were just two target–background orientation combinations in Experiment 2; in both Experiments, the total number of trials was equal. Thus, it may have been the different number of presentations per target–background orientation combination that contributed to learning failure rather than random presentation. For example, in Experiment 1, there were fewer presentations per target–background element combination than in the ordered stimulation in Experiment 2; this might have caused less interference in Experiment 1.

This gap raises the need of a control experiment (Experiment 3), in which only two different background element orientations (and another condition with only 2 target element orientation) are presented randomly as in Experiment 1. Comparison of these results with those of Experiment 2 would reveal whether the randomness itself reduces failure of learning. If the number of presentation per target–background element combination was crucial to failure of learning, then we would observe more frequent failures in Experiment 3 than in the Mixed condition of Experiment 1.

5.2. Methods

Twelve subjects were randomly divided into two conditions: the BGmix condition and TGmix condition (six subjects each). The methods for Experiment 3 were largely the same as those used in Experiment 1, except for the following differences.

In the BGmix condition, one target element orientation was paired with two background element orientations. In the TGmix condition, one background element orientation was paired with two target element orientations. In other words, in each condition, there were two possible combinations of target and background element orientations, in contrast to the eight combinations used in Experiment 1.

In the BGmix condition, the orientation of the background elements in each trial was randomly selected as either vertical or horizontal; the orientation of the three target lines was kept constant, either -45° or 45° from the vertical meridian, and was assigned to each subject prior to the experiment. The orientation of the target element was counterbalanced across subjects.

In the TGmix condition, the orientation of the three target lines in each trial was randomly selected as either -45° or 45° from the vertical meridian; the orientation of the background elements were kept constant, either vertical or horizontal, and was assigned to each subject prior to the experiment. The orientation of the background element was counterbalanced across subjects.

In both conditions, each training session contained 546 trials, which were presented in 21 blocks; the total time to complete the training session was approximately 50 min. Each block contained 26 trials with a constant SOA. Each session started with a longer SOA (180 ms), which was decremented by 20 ms every three blocks, and altogether, a series of seven SOAs (180, 160, 140, 120, 100, 80, 60 ms) was used.

5.3. Results of Experiment 3

We calculated the correct response rate for the orientation discrimination task, irrespective of the orientation combination, for each SOA individually, and averaged the mean correct response rate across subjects for each SOA, as plotted in Fig. 7. Fig. 7A shows the mean for BGmix, and Fig. 7B, the mean for TGmix. The logistic curves fitted to the mean values are for visualization purposes only.

If we combine both conditions to apply 3-way ANOVA with one between (condition; BGmix or TGmix), and two within factors (day and SOA) for correct responses on the discrimination task, the learning effect becomes clearer. There was a significant main effect for day ($F(1, 10) = 35.77$, $p < .001$) and SOA ($F(6, 60) = 98.315$, $p < .001$), and no significant effect for condition ($F(1, 10) = 1.078$, $p = .323$).

Here we looked at each condition. In the BGmix condition, where two background element orientations were randomly presented in trials, the results of a repeated measures ANOVA with two within-subject factors (day and SOA) showed a significant main effect for day ($F(1, 5) = 37.143$, $p = .002$) and SOA ($F(6, 30) = 62.640$, $p < .001$), with no interaction between the factors ($F(6, 30) = .346$, $p = .906$). In the TGmix condition, where two target element orientations were randomly presented in trials, the results of repeated measures ANOVA with two within-subject factors (day and SOA) showed a tendency for day effect ($F(1, 5) = 5.836$, $p = .060$) and significant main effect for SOA ($F(6, 30) = 40.470$, $p < 0.001$). Thus, data analysis for the correct response rate suggests that random presentation of two target–background combinations caused PL. However, failure of learning may be slightly more in the TGmix condition.Next, we analyzed the threshold SOAs in both conditions (Fig. 8). The results of a 2-way ANOVA with one between (condition; BGmix or TGmix) and one within-subjects (day) factor showed a significant main effect for day ($F(1, 10) = 22.563$, $p = .001$), indicating improvement over days, but no significant effect for condition ($F(1, 10) = 1.639$, $p = .229$) and no significant interaction ($F(1, 10) = .931$, $p = .357$). If we look

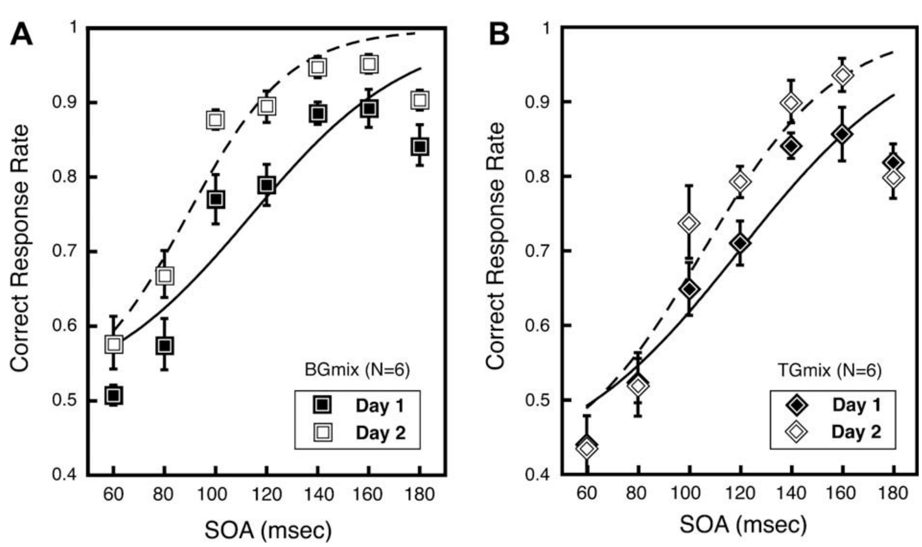

Fig. 7. The mean correct response rate over various SOAs in the BGmix (A) and TG mix (B) in Experiment 3. Filled symbols are for day 1 and open symbols are for day 2. Each logistic curve was fitted to the averaged correct response rate across subjects for day 1 and day 2 in each condition just for visualization purpose only. Error bars represent ±1 standard error of the mean.

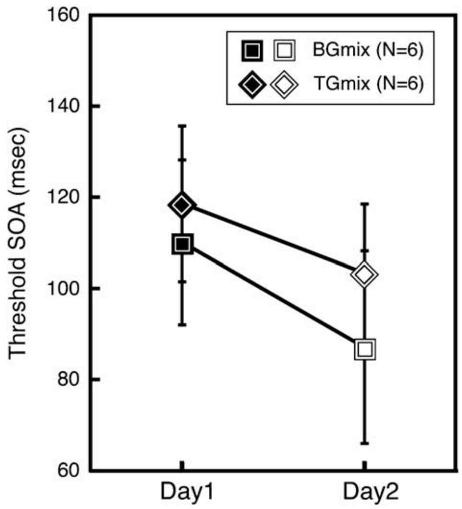

Fig. 8. The mean estimated 75% threshold SOA for the BGmix and TGmix conditions in Experiment 3. Filled symbols are for day 1 and open symbols are for day 2. Error bars represent ±1 standard error of the mean.

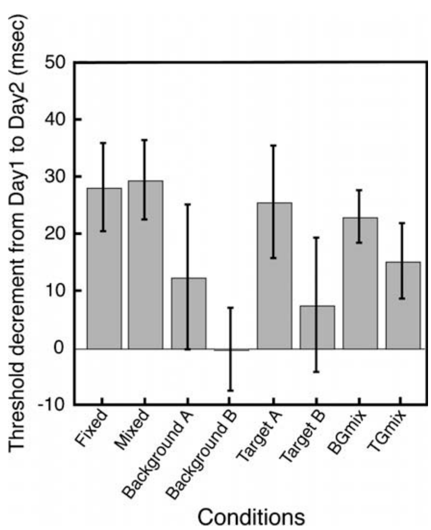

Fig. 9. Comparison of the averaged threshold decrements from day 1 to day 2 for all conditions. Error bars represent ±1 standard error of the mean. Fixed and Mixed are for Experiment 1. Background A, Background B, Target A, and Target B are for blocks A and B in Experiment 2. BGmix and TGmix are for Experiment 3.

at the thresholds in each condition, learning clearly occurred in the BGmix condition (paired sample *t*-test, $t(5) = 5.004$, $p = .004$, the averaged threshold decrement was 23.0 ms, see Fig. 9), by comparison, learning was marginal in the TGmix condition (paired sample *t*-test, $t(5) = 2.305$, $p = .069$, the averaged threshold decrement was 15.3 ms, see Fig. 9).

To summarize the results of Experiment 3, only two combinations of target–background element orientations caused PL. Learning might have been stronger in the BGmix condition, or failure of learning might have occurred more often in the TGmix condition.

6. Discussion

In this study, we examined whether and, if so how, failure (reduction in strength) of PL occurs in TDT (Karni & Sagi, 1991) under roving and successive two-part training conditions. We found that in Experiment 1, roving training, where background and target element orientations were changed in a random order from trial to trial, did not prevent learning from occurring. In Experiment 2, we tested whether interference of learning, as examined in the two-part training paradigm, was related to feature specificity. The important question in Experiment 2 was whether interference in the Background condition was dissociated from the Target condition. We found that they were dissociated; interference occurred when different background element orientations were trained in two successive parts, whereas no interference occurred when different target element orientations were trained in two successive parts. In Experiment 3, we controlled the number of target–background orientation combinations and tested whether roving with two orientation combinations, or a larger trial numbers per target–background orientation combination hinders TDT learning. We found that PL took place both when two background orientations were roving and when two target element orientations were roving, although PL was weak in that latter case.

In short, TDT learning occurred as a result of training where background orientation roved and target element orientation was fixed (the BGmix condition in Experiment 3), but learning did not occur as a result of training where background orientation changed in two-part training and a target element orientation was fixed (the Background condition in Experiment 2). On the other hand, PL also occurred, though weakly, as a result of training where target element orientation roved and background element orientation was fixed (the TGmix condition in Experiment 3), and as a result of training where the target element orientation changed in two-part training and background orientation was fixed (the Target condition in Experiment 2).

6.1. Roving and TDT learning

Previous studies have shown that PL does not occur with roving training (Kuai et al., 2005; Xiao et al., 2008; Yu et al., 2004; Zhang et al., 2008). However, others have shown that in some cases PL does occur with roving, although the strength of learning is comparatively weaker than when training was conducted without roving (Adini et al., 2004; Otto et al., 2006; Tartaglia et al., 2009).

The results of our Experiment 1 clearly demonstrate that TDT training with roving (the Mixed condition) results in strong learning, just as the conventional (Fixed condition) training schedule does. Interestingly, the averaged threshold on day 1 in the Mixed condition was lower than in the Fixed condition in Experiment 1. Although it was not statistically significant, this lower threshold in the Mixed condition may be due to less within-session deterioration since deterioration did not transfer to different target element orientation (Mednick, Arman, & Boynton, 2005). It has been suggested that roving training obstructs learning when it involves with higher-level processing such as decision-making (Adini et al., 2004), stimulus predictability (Zhang et al., 2008), or memory tracing (Kuai et al., 2005; Xiao et al., 2008; Yu et al., 2004). If this is true, then the absence of failure in TDT learning with roving training may indicate that TDT learning does not depend on higher processing, and largely involves early sensory processing.

However, the results of Experiment 3, in which the number of target–background orientation combinations was equal to that in Experiment 2, and was much smaller than in Experiment 1 suggest that roving may slightly impede the higher processing involved in TDT. In Experiment 3, while PL clearly took place when two different background element orientations were randomly interleaved, only marginal PL was observed when two different target element orientations were randomly interleaved. This may indicate that if roving training impedes PL, the impediment may be stronger for targets compared to background in the TDT stimulus. It has been demonstrated that TDT learning is specific to background element

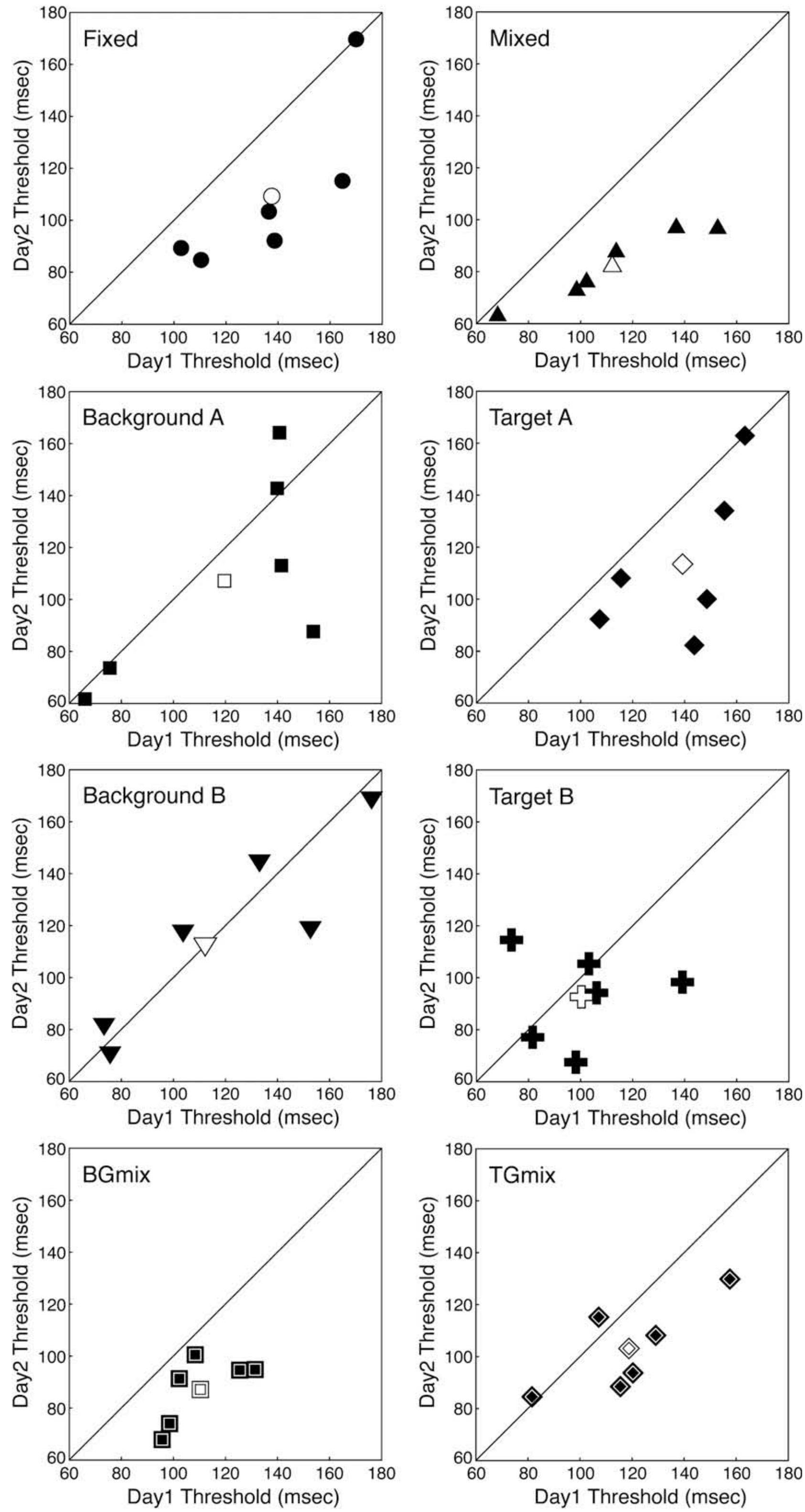

Fig. 10. Comparison of day 1 and day 2 threshold SOA for all subjects in all experiment. In each panel, the *x*-axis shows the threshold SOA for day 1 whereas the *y*-axis shows the threshold SOA for day 2. The data below diagonal lines indicate that learning has taken place. Filled points are individual subjects' data. Open points indicate the averaged value in conditions. The two panels in the top row are for Experiment 1 (the Fixed and Mixed conditions). The two panels in the second row are for block A and the two panels in the third row are for block B in Experiment 2 (the Background and Target conditions). The two panels in the bottom row are for Experiment 3 (the BGmix and TGmix conditions).

orientation but not to target element orientation (Karni & Sagi, 1993). If feature specificity in PL indicates involvement of early neural processing, lack of specificity in target element orientation in TDT may indicate involvement of higher processing, which may be susceptible to roving (Adini et al., 2004; Xiao et al., 2008; Zhang et al., 2008).

6.2. Interference and TDT learning

The results of Experiment 2 indicate that interference occurred in background element orientations, but not in target element orientations in the two-part training. The dissociated results in the Background and Target conditions suggest that, at least in TDT learning, interference is associated with feature specificity. As mentioned above, TDT learning has been shown to be specific to the orientation of background elements of the stimulus, not to the orientation of target element (Karni & Sagi, 1991). Feature specificity is often taken as evidence that learning involves early sensory neural processing areas including the primary visual cortex (V1). A previous neuroimaging study of TDT demonstrated that it is V1 where the main neural change occurs selectively over the course of training (Yotsumoto et al., 2008). Behavioral studies that have employed TDT also indicate that TDT learning involves V1 (Karni & Sagi, 1991) based on a line of evidence including the location specificity of the TDT learning. Thus, it is likely that V1 plays a significant role in TDT learning. Since interference has also been shown to be specific to the background element orientation, it is possible that the interference observed in the present study involves early visual processing.

However, some investigators argue against the general involvement of early sensory processing in PL. For example, it has been suggested that learning basically occurs in a central site, but that the brain also learns to attend to a peripheral location or orientation (Mollon & Danilova, 1996; Xiao et al., 2008). In this view, orientation specificity in TDT would occur because the central site is not well trained to attend to a new orientation and, as a result learning fails in testing with the orientation. In this view, orientation interference would occur when training involving attention to a stimulus with one orientation is interrupted by subsequent training requiring attention to a stimulus with different orientation. While this view is insightful and may well explain PL in some cases (Xiao et al., 2008), it would be difficult from this perspective to provide straightforward explanation for why interference occurred only in the Background condition, and not in the Target condition of Experiment 2. If subjects learned only to attend to a new orientation, interference should not have occurred in both the Background and Target conditions. On the other hand, if attending to a new orientation was not yet learned, interference should have occurred in both the Background and Target conditions. Thus, we would need other factors than attention to interpret our results.

Note it is possible that some higher-stage processing as well as early-stage processing is involved in TDT, as discussed above. Roving may have affected TDT learning when different orientations of target element were randomly interleaved (Experiment 3). Since TDT learning is not specific to the orientation of target elements, the higher-stage neural processing may be required for a target, if the hypothesis that roving impedes higher processing is correct (Adini et al., 2004; Mollon & Danilova, 1996; Xiao et al., 2008; Zhang et al., 2008).

There might be other possibilities for the no-learning effect in the Background condition in Experiment 2. First, one might suggest that the observation of no-learning might be due to a floor effect, not to interference. However, this is not likely. The threshold SOA value in part A in the Background condition of Experiment 2 was comparable to the initial threshold SOA values in other conditions such as the Mixed condition in Experiment 1.

It is also unlikely that the no-learning effect in the Background condition of Experiment 2 is attributable to the number of trials per session or per SOA. First, previous studies have suggested that the number of trials in a training session significantly influences performance improvement. For example, some studies have shown a higher threshold with a larger number of trials (Censor & Sagi, 2008; Censor et al., 2006; Ofen, Moran, & Sagi, 2007). However, the total number of trials in the Background condition in Experiment 2 of our study was equal to the number in the Target condition of Experiment 2; the same total number of trials was used in the Fixed and Mixed conditions in Experiment 1. Second, the number of trials per SOA in part A in the Background condition of Experiment 2 was indeed smaller than that in the Fixed condition in Experiment 1; yet, this cannot explain the no-learning effect in the Background condition of Experiment 2, since the smaller number of trials per SOA would predict smaller adaptation, and thus better performance (Censor et al., 2006). However, performance was better higher in the Fixed condition (Experiment 1) than in the Background condition (Experiment 2) (see Fig. 2 or Fig. 9). Thus, the number of trials in the Background condition of Experiment 2 is not likely to cause the no-learning effect in that condition.

Lastly, one might also argue that the reason learning did not take place in the Background condition of Experiment 2 was that deterioration had occurred (Censor et al., 2006; Censor & Sagi, 2008; Mednick, Nakayama, & Stickgold, 2003; Mednick et al., 2005, 2002, Ofen et al., 2007) as a result of two successive parts of training within a single day. While there seems to be some similarity between what others have reported as deterioration (Mednick et al., 2002, 2003, 2005) and the interference in our study, there is also a clear distinction between these phenomena. In a previous study, Mednick et al. (2005) investigated the time course of deterioration within and across training sessions in 1 day. They found that deterioration transferred to different background orientations but not to different target element orientations. They concluded that deterioration is specific to the orientation of target elements, but is not specific to background orientation.

The results of Mednick et al. are very comparable to some aspects of our results, especially our results from day 1 of Experiment 2, as we found no performance improvement in the second part of the Background condition (where the background orientation was changed), and significant performance improvement in the second part of the Target condition in day 1 (where target orientation was changed). However, what distinguishes our study from the Mednick et al. study emerges in the results acquired on day 2, that is, the effect of sleep. It has been reported that adaptation or deterioration due to over-training in sessions can be transient and that nightly sleep or a nap can facilitate recovery from such over-training (Censor & Sagi, 2008; Censor et al., 2006; Mednick et al., 2002, 2003, 2005). In our study, subjects participated in TDT during two consecutive days, between which they slept at night. If the lack of performance improvement in part B on day 1 in the Background condition of Experiment 2 was due to deterioration by over-training, we would expect to see improved performance on day 2. However, performance did not improve in either part A or part B on day 2 in the Background condition of Experiment 2. Thus, it is highly likely that the no-learning effect seen in the Background condition of Experiment 2 was due to interference caused by training with different background orientations, not due to deterioration (Mednick et al., 2002, 2003, 2005) or adaptation within-sessions (Censor & Sagi, 2008; Censor et al., 2006; Ofen et al., 2007).

Thus, none of the three aforementioned possibilities for the no-learning effect in the Background condition of Experiment 2 is likely. We conclude that the no-learning effect may well be due to interference arising in the two-part training paradigm.

Although the amount of learning in the Target condition of Experiment 2 seems small, especially in day 2 part B, we conclude that learning did occur in that condition. First, in the Target condition, the average number of "correct" trials across various SOAs was significantly larger in both parts A and B on day 2 than on day 1. Second, the averaged threshold in this condition had already improved in part B of day 1 compared to part A. Third, the averaged threshold in part A on day 2 was higher than part A on day 1. Thus, it is likely that learning did occur in the Target condition of Experiment 2, but that the overall amount of learning was small because a plateau was reached.

What is suggested about the mechanism of PL interference? It has been well documented that learning interference takes place in the motor learning domain (Brashers-Krug et al., 1996; Criscimagna-Hemminger & Shadmehr, 2008; Muellbacher et al., 2002; Shadmehr & Holcomb, 1997; Walker et al., 2003; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002). Those studies proposed that interference of motor learning occurs because a dynamic learning process that lasts even after the offset of training is damaged. Interference found in PL of a verniar acuity task (Seitz et al., 2005) suggests that such a long-lasting dynamic learning process occurs in PL as well.

The present study provides further evidence of the possible mechanism of interference in PL. Results from Experiment 2 indicate that in a two-part training paradigm, the latter part of training (in which the orientation of background elements differs from that in the first part of training) interferes with TDT learning in the first part of training. That is, TDT interference is specific to the orientation of background elements in the stimulus. It has also been shown that TDT learning does not transfer to untrained background element orientations (Karni & Sagi, 1991). One of the most likely mechanisms for learning interference is thus as follows: the neural pathway for the trained background orientation is excited, and triggers some kind of inhibition imposed on other neural pathways that correspond to untrained orientations. In a two-part training paradigm like the Background condition we used in Experiment 2, training of vertical background elements orientations, for example, leads to excitation of the vertical orientations along with inhibition of the other orientations. Such excitation and inhibition effects in the first of such a two-part training paradigm is nullified by a subsequent part of training that focuses on horizontal background orientations, which causes excitation of the horizontal background elements and inhibition of the other background orientations including vertical. However, if this is true, why does interference occur in two-part training, as in Experiment 2, but not in training in which two different background element orientations were presented in a random order, from trial to trial, as in Experiment 3? One possible answer to this question is that the excitement associated with the trained orientation can occur immediately but the onset of inhibition on untrained orientations may be delayed. In this way, we may begin to explain why PL interference does not occur when different background element orientations are interleaved and why interference in PL does occur in a two-part training paradigm. Although this study helps us better understand the possible mechanisms at work in PL, future research is necessary to test the validity of the temporal model.

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