The classical TDT perceptual learning is mostly temporal learning

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The seminal study on perceptual learning of TDT (a texture discrimination task) has greatly shaped the field of perceptual learning up to the present time. However, here we demonstrate that this classic learning mostly involves temporal learning, rather than texture discrimination learning. Specifically, observers first practiced a letter identification task with backward masking to saturate the potential temporal learning of target–mask separation in TDT learning before they practiced the backward-masked TDT task directly. The temporal learning accounted for most of the overall TDT improvement, indicating TDT learning being mostly temporal learning. Meanwhile, the location specificity of TDT learning may be interpreted as temporal learning being confined to the trained location with conventional training because learning became mostly location invariant with double training. These results provide a new context to interpret the existing TDT brain imaging data aimed at understanding the neural mechanisms of perceptual learning.

Introduction

In their seminal study Karni and Sagi (1991) reported that perceptual learning of TDT (a texture discrimination task) is specific to the trained retinal location and orientation. This and similar findings of learning specificities at the time (Fiorentini & Berardi, 1980; Ball & Sekuler, 1987; Schoups, Vogels, & Orban, 1995; Crist, Kapadia, Westheimer, & Gilbert, 1997; Fahle, 1997) led to the conclusion that perceptual learning may reflect neural plasticity in the retinotopic early visual cortex, which has deeply impacted the field of perceptual

learning up to the present time. For example, location specificity is used as evidence to support a recent modeling analysis that perceptual learning engages improved probabilistic inference in the early visual areas (Bejjanki, Beck, Lu, & Pouget, 2011).

In a TDT task the texture stimulus consists of a vertical or horizontal target array of oblique bars surrounded by uniform vertical or horizontal bars (Figure 1a). The stimulus is very brief (10 ms) and backward masked. Learning is characterized by reduced texture-mask stimulus onset asynchrony (SOA) threshold for discriminating the orientation of the target array. It is not surprising that TDT learning contains a temporal component in that observers learn to temporally separate the texture from the mask (Schubo, Schlaghecken, & Meinecke, 2001; Censor, Bonneh, Arieli, & Sagi, 2009). However, it has never been questioned whether and how much texture discrimination learning is really involved in this specific TDT learning task after temporal learning is discounted, even if the texture stimulus virtually contains a pop-out target (oblique target bars vs. vertical or horizontal background bars).

In addition, the link between learning specificity and neural plasticity in the early visual areas has been challenged by our recent studies (Xiao et al., 2008; Zhang, Xiao, Klein, Levi, & Yu, 2010; Wang et al., 2012). Location-specific Vernier and contrast learning under conventional training condition (i.e., training at one location and the transfer of learning tested at an untrained location) can often transfer completely to a new retinal location (i.e., a diagonal visual quadrant) if the new location is additionally trained with an irrelevant task (Xiao et al., 2008; Wang et al., 2012),
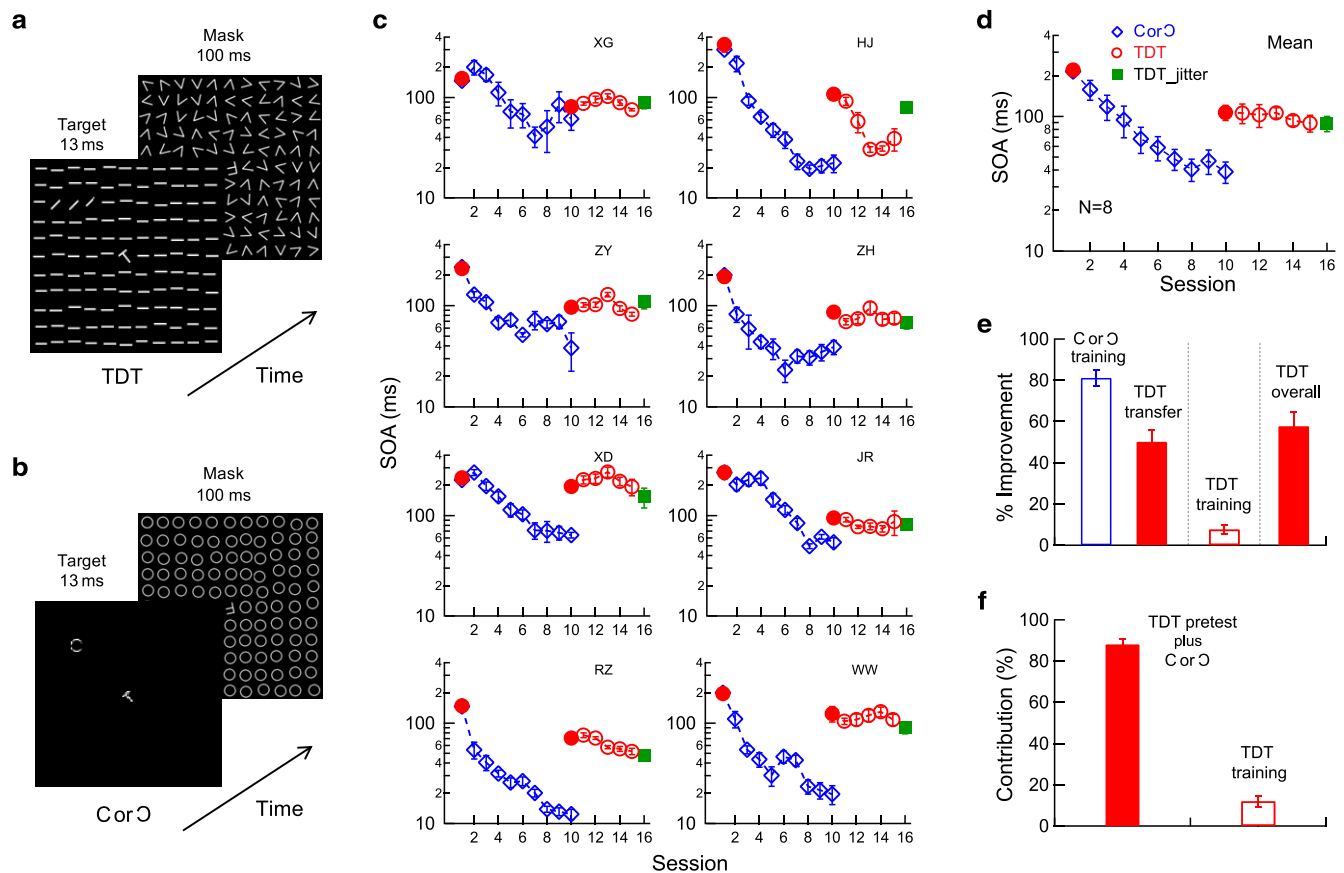
Figure 1. The contribution of temporal learning to TDT learning. (a) TDT stimulus configuration. (b) C/flipped-C stimulus configuration. (c, d) The individual and mean training results: The observers were first trained with the C/flipped-C task for eight sessions. The TDT thresholds were tested before and after this training (five staircases each). The observers then continued to practice TDT for five sessions. After that the TDT thresholds were tested again with the stimulus onset jittered by ±200 ms (six staircases). Each error bar represents 1 standard error of the mean. (e) The mean percent improvements of the initial trained C/flipped-C and untrained TDT (left two bars), the later trained TDT (middle bar), and TDT overall (right bar). (f) The respective contributions to the overall TDT improvement by initial TDT pretest plus C/flipped C training and by later TDT training.

suggesting perceptual learning being a high-level process beyond the retinotopic visual cortex. Therefore, if this "double training" method could enable TDT learning to transfer to untrained locations, the TDT learning would also be a high-level process, and the location specificity would indicate that the temporal learning is confined to the trained location (i.e., spatiotemporal) because of the particular training method.

Methods

Observers and apparatus

Twenty-five observers (undergraduate students in their early 20s) with normal or corrected-to-normal vision participated in this study. All were new to psychophysical experiments and were unaware of the purposes of the study. Informed written consent was obtained from each observer prior to data collection. They practiced for approximately 15 to 20 minutes before data collection.

The stimuli were generated with a Matlab toolbox Psychtoolbox-3 (Pelli, 1997) and presented on a 21-inch Dell P1130 color monitor (1024-pixel × 768-pixel resolution, 0.38-mm × 0.38-mm pixel size, 150-Hz frame rate for texture stimuli and 120-Hz frame rate for orientation stimuli; Dell Computer Corporation, Round Rock, TX). The mean luminance of the monitor was 34 cd/m^2. The luminance of the monitor was linearized by an 8-bit look-up table. A chin- and headrest helped stabilize the observer's head. Experiments were run in a dimly lit room, and viewing was monocular.

Stimuli

The texture stimulus (Figure 1a) was nearly identical to the original one used by Karni and Sagi (1991). It

consisted of a 19 × 19 array of white line segments (34 cd/m^2) centered on a black screen background (0.5 cd/m^2) and occupied a 14° × 14° area at a viewing distance of 1.14 m. The line segments were 0.42° × 0.03° each and spaced 0.73° apart from center to center. The position of each line segment was jittered slightly from trial to trial by 0° to 0.10°. The target was a vertical or horizontal array of three oblique line segments surrounded by uniform vertical or horizontal bars. The target array was presented at one visual quadrant, 4° to 6.5° from the texture center. In addition, a randomly oriented letter T or L (0.44° × 0.34°) was presented at the center of the texture to control fixation (TDT data with letter identification rate less than 90% would be discarded). The mask was a same-sized field consisting of 19 × 19 randomly oriented V-shaped patterns.

The orientation stimulus (Figure 2c) was a Gabor patch (Gaussian enveloped sinusoidal grating) with a spatial frequency at 1.5 cpd, standard deviation at 0.24°, contrast at 0.47, and phase randomized for every presentation. The Gabor patch was presented on a mean luminance screen background and was centered on a visual quadrant at 5.6° retinal eccentricity. The stimulus was viewed through a circular aperture (diameter = 17°) of a black cardboard that covered the entire monitor screen. This control prevented observers from using monitor edges as external references to determine the stimulus orientation.

Procedure

In a texture discrimination trial, the texture stimulus was flashed for 13 ms, similar to the 10 ms target duration in the original Karni and Sagi (1991) study, which was followed by a 100-ms mask at various SOAs. The observers were asked to make two responses after each trial: first to report the foveal letter (T or L) for fixation control and then to report the orientation of the target array (horizontal or vertical). An auditory feedback was given only for incorrect foveal letter identification. A fixation cross was present for 400 ms and disappeared 500 ms before the onset of the texture stimulus in each trial.

In an orientation discrimination trial, the reference (36° or 126°) and test (reference ± an orientation offset) stimuli were separately presented in two 100-ms stimulus intervals in a random order separated by a 500-ms interstimulus interval. An observer's task was to judge which stimulus interval contained a more clockwise stimulus. Auditory feedback was given upon an incorrect response. A small fixation point preceded each trial by 500 ms and stayed through the trial.

The SOA thresholds and orientation thresholds were estimated with a 2AFC staircase procedure. The staircases followed a 3-down-1-up staircase rule that

resulted in a 79.4% convergence rate. The initial target–mask SOA or orientation difference was sufficiently large, so that the observers could make a correct response easily. The step size of the staircase was 0.05 log units. Each staircase consisted of four preliminary reversals and six experimental reversals (approximately 50 trials). The geometric mean of the experimental reversals was taken as the threshold for each staircase run. An observer typically completed 16 staircases in one 1.5-hour training session.

Results

Experiment 1: The contribution of temporal learning to TDT learning

To quantitatively measure the contribution of temporal learning to TDT learning, we designed a new backward masking task that replaced the texture stimulus with a C/flipped-C letter of the same duration (13 ms) presented at the same location of the TDT target array on a clear screen (i.e., no surrounding stimuli; Figure 1b). As in a TDT task, there was a central letter identification task (T or L) to control fixation. The stimulus was masked by a field of circles presented for 100 ms at various SOAs. Observers were asked to first identify the same central letter (T or L), and then to report whether the peripheral letter was a C or flipped C. The C/flipped-C configuration contained no texture or even line orientation. But it shared the temporal aspect of the TDT stimulus in that the observers also needed to temporally separate the target from the mask.

We first measured the TDT pretraining SOA threshold in each observer (five staircases). Then we kept this SOA value fixed and measured the size threshold of C/flipped-C letters for letter identification with a staircase procedure. With the letter size fixed at the just measured threshold (mean = 26.4 ± 1.5 arcmin), the pretraining SOA thresholds and thus the difficulties of the TDT task and the C/flipped-C task were matched. The observers then practiced backward-masked C/flipped-C identification for eight sessions, which minimized C/flipped-C SOA thresholds (Figure 1c and d; the mean percent improvement [MPI] = 81.1 ± 4.1%, $p < 0.001$). The thresholds reached a floor level in the last two sessions, indicating optimal C/flipped-C identification and possibly optimal target–mask temporal separation. Importantly, after the C/flipped-C training the average TDT threshold was halved (Figure 1c and d; MPI = 50.1% ± 5.8%, $p < 0.001$), demonstrating the involvement of temporal learning in TDT learning (similar improvement would thus be expected from TDT training to C/flipped-C
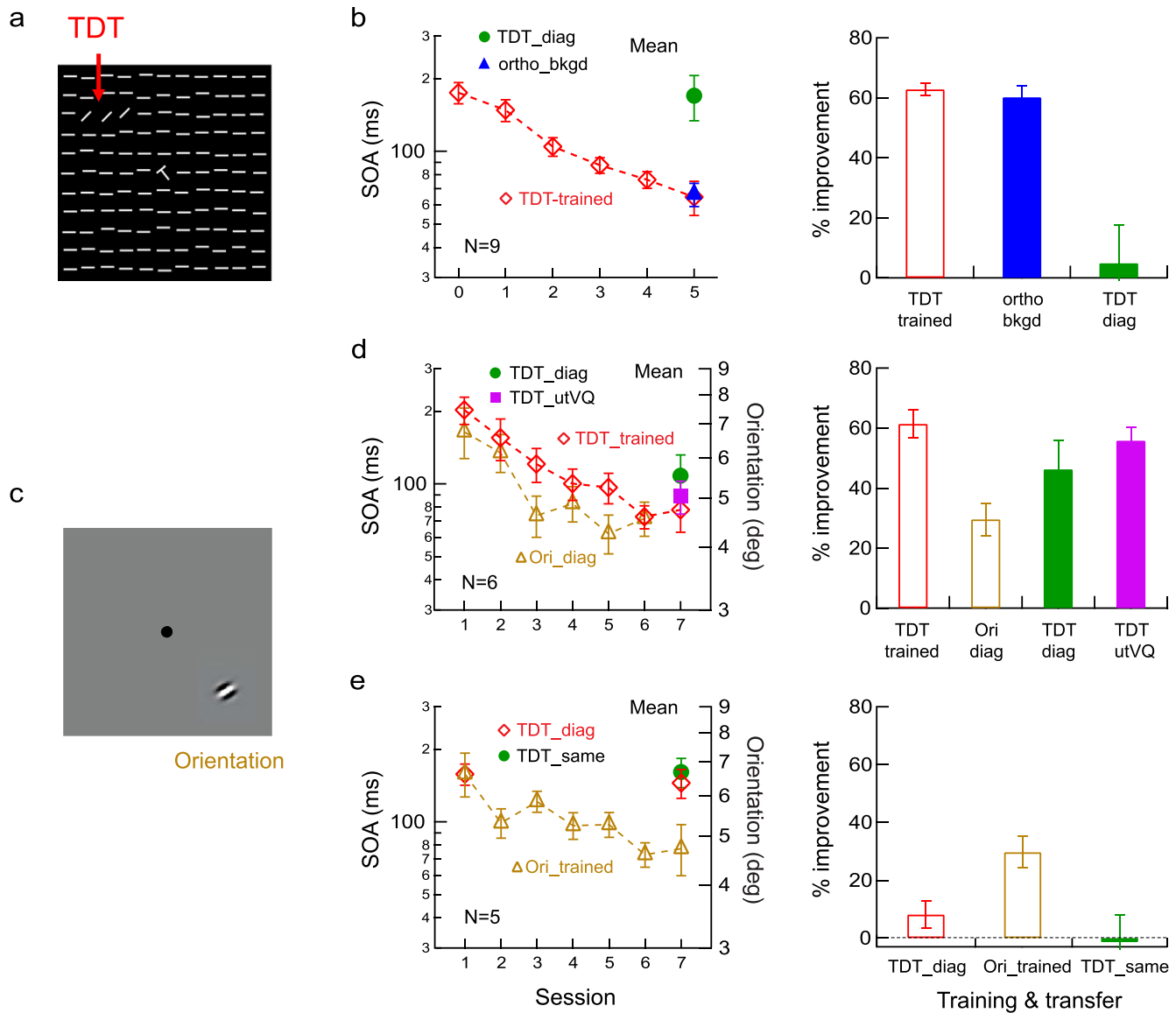
Figure 2. The transfer of TDT learning after double training. (a) TDT stimulus configuration. (b) Baseline: TDT was trained at one visual quadrant and the transfer of learning was tested at an untrained orthogonal background orientation (Ortho_bkgd) and at a diagonal quadrant. Left: mean session-by-session threshold changes; right: mean percent improvements with baseline training. (c) The orientation stimulus. (d) Double training: TDT was practiced at one quadrant and orientation discrimination was practiced at a diagonal quadrant in alternating staircases, and the transfer of TDT learning was tested at the diagonal quadrant and completely untrained quadrants (utVQ) across the horizontal and vertical medians at the same retinal eccentricity. Left: mean session-by-session threshold changes; right: mean percent improvements with double training. (e) Control: only orientation discrimination was trained at one quadrant, and the pre- and posttraining TDT thresholds were tested at the same quadrant and a diagonal quadrant. Left: mean session-by-session threshold changes; right: mean percent improvements with control training. Each pretest and posttest included five staircases.

performance). In Figure 2e we show that the TDT pretest per se would reduce the thresholds by approximately 8% under a comparable condition (i.e., same number of staircases in pretest and a multi-session gap between the pretest and posttest). Assuming the same amount of contribution of the pretest here, the C/flipped-C training would actually reduce the TDT threshold by 42.1%.

The next step was critical! To determine how much texture discrimination learning was truly involved in TDT learning, we had the same observers continue to practice TDT for five sessions. However, this direct TDT training improved the TDT performance by merely $7.6\% \pm 2.2\%$ ($p = 0.006$, Figure 1c and d) when compared with TDT thresholds after the C/flipped-C training. There were virtually no threshold changes in

most observers (Figure 1c). The combined TDT improvement (MPI = 57.7% ± 7.2%, $p < 0.001$) after two stages of practice was similar to the improvement in the baseline condition in which only TDT was solely trained (data presented in Figure 2b; MPI = 62.7% ± 2.0%, $p < 0.001$). Overall, the initial TDT pretest and the C/flipped-C training contributed 14.1% and 74.0% of the total TDT improvement; whereas, the later direct TDT training contributed the remaining 11.9% (Figure 1f). Since it is reasonable to assume that the TDT pretest also induced at least some temporal learning, these results indicate that approximately 74% to up to 88.1% (14.1% + 74.0%) of the TDT learning was due to temporal learning. On the other hand, the T or L identification rate was not significantly changed after training (95.7% ± 1.4% pretest vs. 96.6% ± 1.1% posttest), indicating that the TDT learning was not due to deviated eye fixations.

We also excluded the possibility that TDT training led to more precise timing to the onset of the brief stimulus, rather than better target–mask separation in perception. After the observers completed the two-stage training, the TDT thresholds were measured again with the onset of the texture stimulus altered by ±200 ms to interrupt onset timing. However, this manipulation had no impact on the TDT performance (TDT thresholds at 16th vs. 15th session, $p = 0.38$; Figure 1c and d), suggesting that TDT training more likely improved target–mask separation.

Experiment 2: The removal of location specificity in TDT learning with double training

In this experiment we tested whether location specificity in TDT learning could be removed with a variation of the double training method (Wang, Zhang, Klein, Levi, & Yu, 2010; Zhang, Wang, Klein, Levi, & Yu, 2011). This new double training method paired location-nonspecific learning, such as orientation learning (Zhang, Xiao, et al., 2010), with highly location-specific learning, such as Vernier learning, to actuate the latter learning to transfer all over the visual field at completely untrained retinal locations and different eccentricities. This was a test of our hypothesis that location specificity suggests TDT temporal learning being confined to the trained location in conventional training, as well as a direct challenge to the link between TDT learning and V1 plasticity built on the basis of location specificity (Karni & Sagi, 1991). In addition, in the original report, TDT learning was found to be specific to the background bar orientation of the texture stimulus but not to the target bar orientation (Karni & Sagi, 1991). However, if TDT learning was mostly temporal learning as Figure 1

indicates, we would not expect much orientation specificity.

We first measured the location and orientation specificities in a baseline condition in which only the TDT was practiced. Nine observers learned TDT at one visual quadrant for five sessions (MPI = 62.7% ± 2.0%, $p < 0.001$), but learning transferred little to the untrained diagonal visual quadrant (MPI = 4.9% ± 12.6%, $p = 0.36$; Figure 2b), replicating the original results that TDT learning was highly specific to the trained location (Karni & Sagi, 1991). However, TDT learning transferred completely when the orientation of the background bars was rotated by 90° (MPI = 60.1% ± 4.0%, $p < 0.001$; Figure 2b), as predicted if TDT learning mostly involved temporal learning.

In a double training scheme, six new observers practiced TDT at one visual quadrant (MPI = 61.4% ± 4.7%, $p < 0.001$) as well as orientation discrimination with a Gabor patch at the diagonal transfer quadrant (MPI = 29.5% ± 5.5%, $p = 0.006$) in alternating blocks of trials (Figure 2c). After this double training, TDT learning transferred not only to the diagonal quadrant where orientation was trained (MPI = 46.2% ± 9.6%, $p = 0.002$), consistent with previous double training results (Xiao et al., 2008; Wang et al., 2012), but also to completely untrained visual quadrants (utVQ) across the horizontal and vertical medians at the same eccentricity (combined MPI = 57.5% ± 3.6%, $p < 0.001$), consistent with our recent finding that orientation learning in double training can actuate a high location specific learning to transfer to untrained visual quadrants (Wang et al., 2010; Zhang et al., 2011). These results suggest that TDT temporal learning is not necessarily confined to the trained location. It can be mostly purely temporal and transferrable to untrained retinal locations.

A control experiment in which five new observers only practiced orientation discrimination at one quadrant (MPI = 29.7% ± 5.2%, $p = 0.002$) found no TDT improvement at the same quadrant (MPI = −1.4% ± 18.1%, $p = 0.53$) and the diagonal quadrant (MPI = 8.1% ± 7.7%, $p = 0.18$; Figure 2e), indicating that orientation training per se had no impact on TDT performance at the same or a different retinal location. It was only in double training that orientation training could enable the transfer of TDT learning.

It is worth noting that the C/flipped-C task in Experiment 1 may not be considered as the second (location training) task in double-training. The location training task in double-training has to be an irrelevant one. For example, in the control condition (Figure 2e) orientation learning per se had no impact on TDT performance at either the same or a diagonal quadrant. In contrast, the C/flipped-C task affected TDT performance directly. Hence it was a relevant task and shared at least some of the mechanisms.
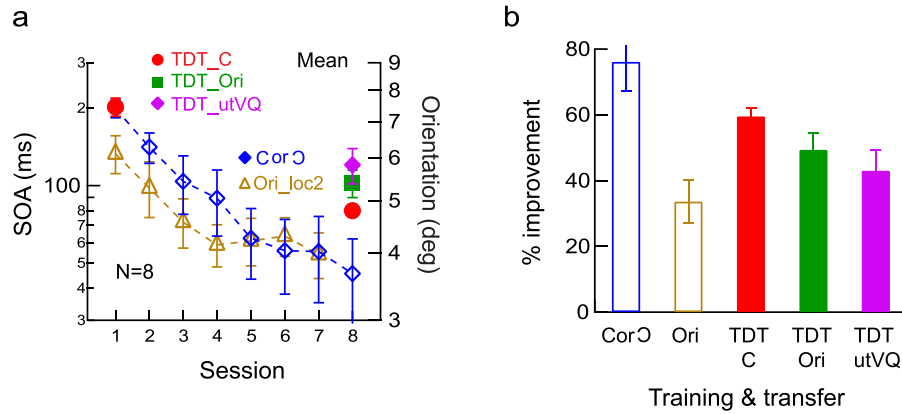
Figure 3. TDT improvement after C/flipped-C and orientation double training. (a) Mean session-by-session threshold changes of C/flipped-C identification at one visual quadrant and orientation discrimination at a diagonal quadrant, as well as TDT pretraining performance at the C/flipped-C trained quadrant (TDT_C) and posttraining performance at the C/flipped-C trained quadrant, the orientation trained quadrant (TDT_Ori) and a completely untrained quadrant at the same eccentricity (TDT_utVQ). (b) A summary of performance improvement due to training and transfer. Each pretest and posttest included five staircases.

Experiment 3: TDT improvement after C/flipped-C and orientation double training

This experiment used C/flipped-C and orientation double training to further demonstrate that TDT learning was mostly temporal learning, rather than texture discrimination learning. Eight new observers practiced the same backward-masked C/flipped-C identification task (MPI = 76.1% ± 8.9%, $p < 0.001$) at one quadrant and orientation discrimination task (MPI = 33.6% ± 6.6%, $p < 0.001$) at a diagonal quadrant, in alternating blocks of trials for five sessions (Figure 3). The TDT threshold at the C/flipped-C trained quadrant was measured before training as the pretraining baseline. After C/flipped-C and orientation double training, TDT performance was improved at the same quadrant where C/flipped-C was trained (TDT_C, MPI = 59.5% ± 2.4%, $p < 0.001$), as much as the improvement after baseline TDT training in the earlier experiment (62.7% ± 2.0%, Figure 2b; $p = 0.32$, two-sample two-tailed t-test), providing further evidence that TDT learning was mostly temporal learning. TDT performance was also improved at the diagonal quadrant where orientation was trained (TDT_Ori, MPI = 49.3% ± 5.2%, $p < 0.001$), as well as at a completely untrained visual quadrant across the vertical median of the C/flipped-C trained quadrant at the same eccentricity (TDT_utVQ, MPI = 49.1% ± 2.1%, $p < 0.001$), comparable to the improvements after earlier TDT + orientation double training (MPI = 45.1 ± 9.5%, Figure 2d). Because the TDT task was not trained at all in this experiment, and orientation training alone could not change TDT performance as previously demonstrated (Figure 2e), TDT improvements at all three locations after this new double training had to be a result of the transfer of C/flipped-C

temporal learning. Therefore, these results confirm our general conclusion that TDT learning is mostly temporal learning, and such learning is transferrable to untrained locations with proper training procedures.

Discussion

Our results demonstrate that most TDT learning is not about texture discrimination but about temporal separation of the very brief target and the mask. TDT training may have increased the speed of temporal processing (Polat, 2009; Sterkin, Yehezkel, Bonneh, Norcia, & Polat, 2009) or narrowed the temporal window of attention (temporal resolution), so that the target could be separated from the mask at shorter SOAs. Moreover, the double training experiment enabled significant transfer of TDT learning to untrained visual quadrants, suggesting that location specificity is an indication of TDT temporal learning being confined to the trained location upon conventional training, rather than of learning occurring in the retinotopic early visual cortex.

The broad learning transfer suggests that TDT temporal learning, like location-specific Vernier and contrast learning that also showed complete learning transfer with double training (Xiao et al., 2008; Wang et al., 2012), is a high-level learning process that occurs at a stage of brain processing beyond the retinotopic visual cortex. Why is perceptual learning location specific in the first place with conventional training? We hypothesized that focused spatial attention to the trained location during multiple sessions of practice could impair the functional connections between high-level learning and the sensory inputs at the untrained

retinal locations to prevent learning transfer, likely by suppressing the untrained retinal locations (Xiao et al., 2008; Zhang, Zhang, et al., 2010). This hypothesis is consistent with neurophysiological and brain imaging findings that spatial attention inhibits unattended locations (Moran & Desimone, 1985; Treue, 2001; Slotnick, Schwarzbach, & Yantis, 2003), even if these locations are unstimulated (Smith, Singh, & Greenlee, 2000; Shmuel, Augath, Oeltermann, & Logothetis, 2006), as is typical in perceptual learning studies. Indeed, our recent event-related potentials (ERP) evidence indicates that location specificity in Vernier learning is associated with suppressed visual N1 suppression corresponding to the untrained transfer location (Zhang, Cong, Song, & Yu, 2013). It is likely that frequent inhibition during multiple sessions of training could produce long-term depression–like behavior at the untrained locations.

Location specificity in TDT learning has also been recently attributed to orientation selective adaptation (Harris, Gliksberg, & Sagi, 2012). When mixed with TDT practice trials, task-irrelevant dummy trials with textures oriented 45° away from the trained TDT stimulus, which supposedly release adaptation with the latter, enable TDT learning transfer to other retinal locations. But dummy trials with orthogonal textures, which supposedly have no impact on TDT adaptation, fail to enable learning transfer. However, in our study the broad TDT learning transfer enabled by Gabor orientation learning at a diagonal quadrant on an otherwise clear screen (Figure 2) was not expected to affect the status of orientation selective adaptation with the TDT stimuli. Moreover, TDT performance was improved, as much as it was directly trained, at two diagonal quadrants where C/flipped-C identification (temporal training) and Gabor orientation discrimination (location training) were trained, respectively (Figure 3). In this extreme case the TDT task was not directly trained, so that no TDT adaptation was possibly involved, but temporal learning represented by TDT improvement transferred.

It is unclear what exact neural mechanisms underlie TDT temporal learning. Recent neurological and functional magnetic resonance imaging (fMRI) studies indicate that the temporal parietal junction as part of the "when" pathway is specifically involved in the judgment of visual temporal orders (Battelli, Cavanagh, Martini, & Barton, 2003; Davis, Christie, & Rorden, 2009). Therefore, TDT learning could result from training-improved processing speed or temporal resolution of neurons and/or circuits in the temporal parietal junction. In addition, consistent with our theory that perceptual learning reflects improved perceptual decision-making in high-level brain areas (Zhang, Zhang, et al., 2010), recent fMRI evidence suggests that perceptual learning involves higher decision-making areas such as the anterior cingulate cortex (Kahnt, Grueschow, Speck, & Haynes, 2011). These areas may also be involved to improve decision making on target–mask temporal separation.

The demonstration of TDT learning being mostly temporal learning allows us to understand in a new context the recent ERP data on TDT learning from the Sagi group (Censor et al., 2009). They reported that TDT performance at various target–mask SOAs correlated to the occipital N1 responses to the mask, but not to the occipital N1 responses to the texture target. Moreover, perceptual learning also enhanced the occipital N1 responses to the mask only. These ERP results not only suggest temporal learning as the authors suggest, but also mirror our behavioral results that there is not much learning of texture discrimination in a TDT learning task.

Our results also provide interesting insight into fMRI evidence with TDT learning by Yotsumoto, Watanabe, and Sasaki (2008). They found that V1 is activated after TDT practice begins, even before any performance gain. However, 2 weeks after training the V1 blood oxygenation level dependent (BOLD) responses are back to the pretraining baseline while TDT performance stays at the posttraining level. The V1 BOLD responses being uncorrelated to TDT performance, in the context of our findings, may suggest that it instead indicates an observer's effort to spatiotemporally attend to the brief and backward-masked texture target, which would activate the activities of the corresponding V1 region (Gandhi, Heeger, & Boynton, 1999). It thus makes sense that V1 BOLD responses increase ahead of TDT performance change. On the other hand, a near-threshold stimulus becomes suprathreshold after training that requires less attention, so that performance can remain at the optimal posttraining level, but V1 is no longer activated, which is consistent with a recent report that the connectivity between the trained visual areas and fronto-parietal attention areas becomes decoupled after perceptual learning (Lewis, Baldassarre, Committeri, Romani, & Corbetta, 2009). This claim of V1 being modulated by learning, rather than being the site of learning per se, is conceptually consistent with recent neurophysiological evidence that the enhanced V1 responses to a contour stimulus after training in awake monkeys are nullified when the monkeys are under anesthesia (Li, Piech, & Gilbert, 2008).

Acknowledgments

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