Perceptual learning of basic visual features remains task specific with Training-Plus-Exposure (TPE) training

Lin-Juan Cong* Department of Psychology, Peking University, Beijing, China

Ru-Jie Wang* Department of Psychology, Peking University, Beijing, China

Cong Yu Department of Psychology, IDG/McGovern Institute for Brain Research, and Peking-Tsinghua Center for Life Sciences, Peking University, Beijing, China

Jun-Yun Zhang Department of Psychology, Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, China

Visual perceptual learning is known to be specific to the trained retinal location, feature, and task. However, location and feature specificity can be eliminated by double-training or TPE training protocols, in which observers receive additional exposure to the transfer location or feature dimension via an irrelevant task besides the primary learning task Here we tested whether these new training protocols could even make learning transfer across different tasks involving discrimination of basic visual features (e.g., orientation and contrast). Observers practiced a near-threshold orientation (or contrast) discrimination task. Following a TPE training protocol, they also received exposure to the transfer task via performing suprathreshold contrast (or orientation) discrimination in alternating blocks of trials in the same sessions. The results showed no evidence for significant learning transfer to the untrained near-threshold contrast (or orientation) discrimination task after discounting the pretest effects and the suprathreshold practice effects. These results thus do not support a hypothetical task-independent component in perceptual learning of basic visual features. They also set the boundary of the new training protocols in their capability to enable learning transfer.

Introduction

Visual perceptual learning improves discrimination of basic visual features (e.g., contrast, orientation, spatial frequency, direction, etc.). The learning often shows specificity not only to the trained retinal location and feature dimension (e.g., Ahissar & Hochstein, 1997; Ball & Sekuler, 1982; Fiorentini & Berardi, 1980; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992; Yu, Klein, & Levi, 2004), but also to the trained task (e.g., Ahissar & Hochstein, 1993; Saffell & Matthews, 2003; Shiu & Pashler, 1992; Zhang et al., 2010).

However, location and feature-specific perceptual learning can be rendered transferrable with new training protocols. Specifically, location specific perceptual learning, such as Vernier, contrast, orientation, and texture discrimination learning, can significantly, and often completely, transfer to untrained retinal locations after double training, in which observers receive additional training of an irrelevant task at the transfer location (Hung & Seitz, 2014; Mastropasqua, Galliussi, Pascucci, & Turatto, 2015; Wang, Cong, & Yu, 2013; Wang, Zhang, Klein, Levi, & Yu, 2012, 2014; Xiao et al., 2008). Similarly, perceptual learning can also transfer to an orthogonal orientation or an opposite direction with a training-plus-exposure (TPE) design, in which observers receive exposure to the transfer orientation/direction through an irrelevant task (Zhang, Cong, Klein, Levi, & Yu, 2014; Zhang et al., 2010; Zhang & Yang, 2014). In both cases the irrelevant secondary task can be performed within the same sessions with the primary

Citation: Cong, L.-J., Wang, R.-J., Yu, C., & Zhang, J.-Y. (2016). Perceptual learning of basic visual features remains task specific with Training-Plus-Exposure (TPE) training. *Journal of Vision*, *16*(3):13, 1–9, doi:10.1167/16.3.13.

doi: 10.1167/16.3.13 Received February 21, 2015; published February 12, 2016 ISSN 1534-7362

learning task, or in later sessions. These new findings suggest that perceptual learning is primarily a rule-based, high-level learning process that occurs beyond the retinotopic and feature-selective visual areas (Zhang et al., 2010). Please note that for historical reasons, we have been using double training and TPE to name the techniques that enable location and feature transfer of learning, respectively. Our recent evidence indicates that these two techniques are essentially the same because the real role of the irrelevant task in both techniques is to expose observers to the transfer location or feature dimension regardless of whether the secondary task is trained (VSS abstracts: Xiong, Zhang, & Yu, 2015; Yu, Xiong, & Zhang, 2015).

In this study we investigated whether the new training protocols could even enable perceptual learning to transfer to a different task. By "different" we mean that the two tasks are completely independent of each other, judged by insignificant transfer of learning in both directions with regular training. For example, in a previous study we found that perceptual learning of foveal orientation and contrast discrimination cannot transfer to each other (Zhang et al., 2010). Here we tested whether cross-task transfer of learning of these two basic visual features is feasible with TPE training. By doing so we essentially tested whether there is a general task-independent component of perceptual learning of basic visual features that is not evident with regular training. These experiments would define the boundary of learning transfer enabled by the new training protocols, and provide new insights into the mechanisms of perceptual learning.

Methods

Observers and apparatus

Thirty-four paid observers (14 males and 20 females, mean age = 22.5 years, $SD = 2.3$ years) with normal or corrected-to-normal vision participated in this study. They were naïve to the purpose of the experiments and were inexperienced in psychophysical observations. Informed written consent with Peking University IRB approval was acquired from each observer before the experiments started.

The experimental setup and stimuli were mostly the same as those in our previous study (Zhang et al., 2010). The stimuli were generated by a Matlab-based WinVis program (Neurometrics Institute, Oakland, CA) and presented on a 21-in. CRT monitor (1024 pixel $\times$ 768 pixel resolution; 0.38 mm $\times$ 0.38 mm pixel size; 120 Hz frame rate; 53.7 cd/m^2 mean luminance). Viewing was binocular at a distance of 3 m, with the head of the observer stabilized by a chin-and-head rest. Experiments were run in a dimly lit room.

Stimuli and procedure

Training involved a contrast discrimination task and an orientation discrimination task, in which observers judged which of the two consecutively presented stimuli had higher contrast or more clockwise orientation. The stimuli were foveal Gabors presented on a mean luminance screen background. The Gaussian envelope of the Gabor function had a standard deviation at 0.17°. The sinusoidal grating carrier had a spatial frequency at 6 cpd, contrast at 0.47, orientation at 36°. The phase of the carrier was fixed at 90° in the contrast discrimination task, and was randomized every presentation in the orientation discrimination task.

The contrast and orientation discrimination thresholds were estimated with a 2IFC staircase procedure. In each trial, the reference and test stimuli were separately presented in two 92-ms stimulus intervals in a random order. The stimulus intervals were separated by a 500-ms interstimulus interval. A fixation cross preceded each trial by 300 ms and disappeared 250 ms before the onset of the first stimulus interval. Observers judged which stimulus interval contained a higher contrast (contrast discrimination) or a more clockwise orientation (orientation discrimination). Auditory feedback was given on incorrect responses.

The staircases followed a three-down-one-up staircase rule to reach a 79.4% convergence rate. Each staircase consisted of four preliminary reversals and six experimental reversals (approximately 50 trials). The initial stimulus difference was sufficiently large so that observers could easily make a correct discrimination. The step size of the staircases was 0.05 log units. The geometric mean of the experimental reversals was taken as the threshold in a staircase run.

The basic experimental design is represented schematically in Figure 1. Experiments 1 and 2 (except for the control conditions) each consisted of 13 daily sessions, including one pretest session (S1), five training-plus-exposure (TPE) sessions (S2-6), one posttest session (S7), and five additional transfer-task training sessions (S8-13). Each session took approximately 1 $\sim$ 1.5 hr to complete. The pre- and posttest sessions each consisted of two conditions: near-threshold contrast and near-threshold orientation discrimination. Each condition consisted of six blocks of trials. The two conditions were performed in alternating blocks of trials (i.e., staircases in an ABBAABBA order to minimize the order effect). In the TPE sessions (S2-6), observers in Experiment 1 practiced near-threshold orientation discrimination for

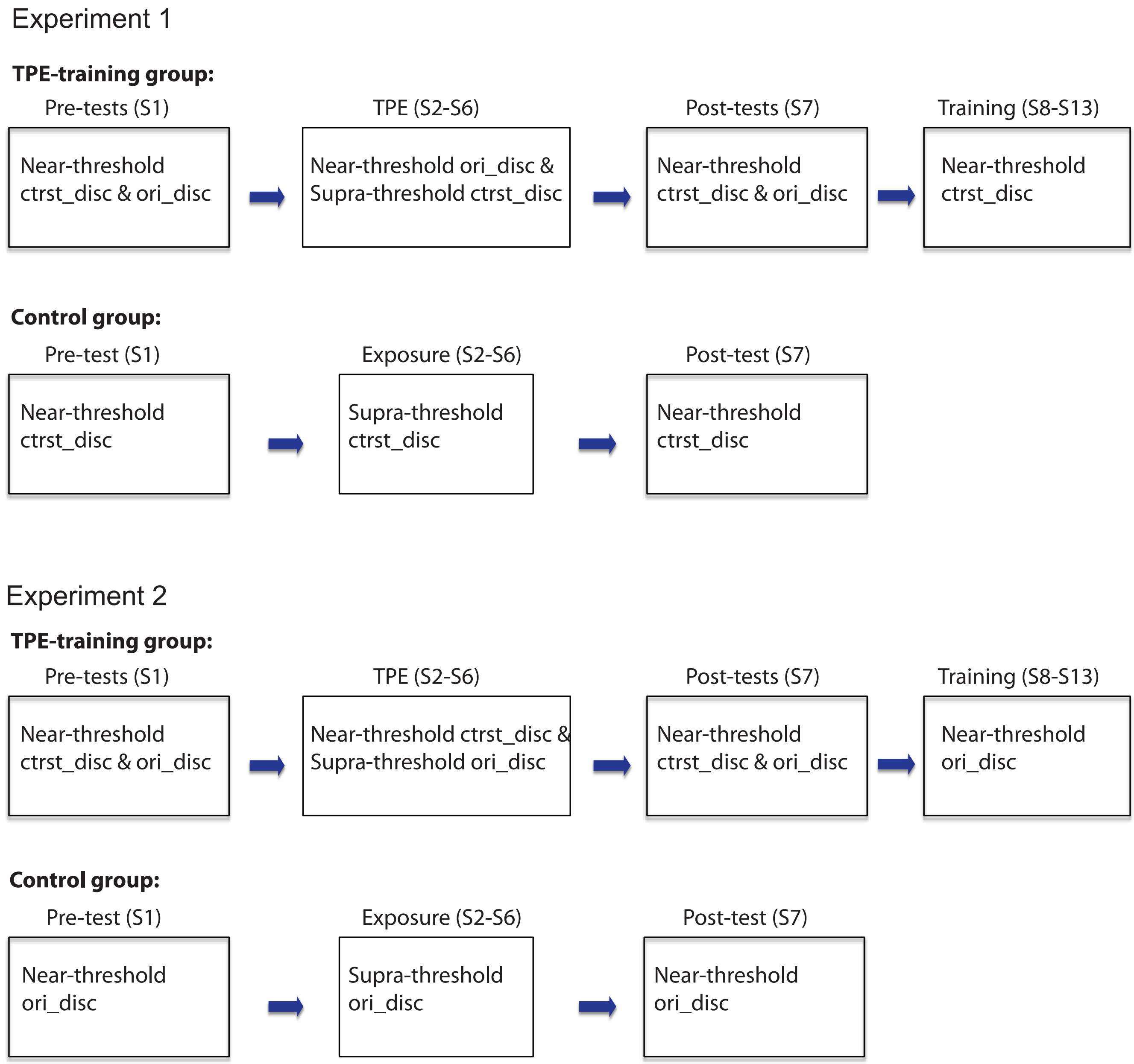

Figure 1. A schematic illustration of the basic experimental design. Ctrst = contrast; ori = orientation; disc = discrimination.

10 staircases, and suprathreshold contrast discrimination with the stimulus contrast difference at 4.5 times the pre-training contrast threshold for 10 blocks (50 trials per block). Observers in Experiment 2 practiced near-threshold contrast discrimination for 10 staircases, and suprathreshold orientation discrimination with the stimulus orientation difference at 4.5 times the pretraining orientation threshold for 10 blocks (50 trials per block). The two tasks were performed in alternating blocks of trials in each session. In the following transfer-task training sessions (S8-13), observers practiced near-threshold contrast discrimination in Experiment 1 or near-threshold orientation discrimination in Experiment 2, for 20 staircases per session.

The control conditions for Experiments 1 and 2 each consisted of seven daily sessions, including one pretest session (S1), five exposure sessions (S2-6), and one posttest session (S7). In Experiment 1 observers performed near-threshold contrast discrimination in the pre- and posttest sessions, and suprathreshold contrast discrimination in the exposure sessions. In Experiment 2 observers performed near-threshold orientation discrimination in the pre- and posttest sessions, and suprathreshold orientation discrimination in the exposure sessions.

Results

Experiment 1: The cross-task learning transfer from orientation discrimination to contrast discrimination with TPE training

Previously we have shown that perceptual learning of near-threshold orientation discrimination with a foveal Gabor stimulus did not significantly improve near-threshold contrast discrimination with the same Gabor (Zhang et al., 2010). Here following a variation of the TPE protocol, observers practiced the same near-threshold orientation discrimination task as in Zhang et al. (2010; Figure 2a). In addition, they also performed suprathreshold contrast discrimination in the same sessions to receive exposure to the contrast discrimination task. The hypothesis here is that the brain network for processing an untrained task may not be readily activated to receive learning transfer from a trained task, which can be remedied by a suprathreshold task. After this TPE training, the orientation discrimination threshold was improved by 34.6% ± 6.0% ($p < 0.001$, one-tailed paired t test in this and later analyses unless otherwise specified, Figure 2b), and the contrast discrimination threshold was improved by 19.5% ± 6.5% ($p = 0.010$, Figure 2b). The accuracy of suprathreshold contrast discrimination remained unchanged from 97.9% to 97.2%. The same observers then practiced near-threshold contrast discrimination, which further improved contrast threshold by 14.5% ± 3.8% relative to the previous TPE training effect (S13 vs. S7; $p = 0.003$, Figure 2b), for a total improvement of 34.0% ± 6.4% (S13 vs. S1). We used a "transfer index" (TI) to gauge the cross-task learning transfer, in which TI = threshold improvement after TPE/total threshold improvement. This TI = 0.50 ± 0.17, which was significantly different from TI = 0 ($p = 0.023$) and from TI = 1 ($p = 0.024$), indicating potential partial learning transfer.

However, even this initial TPE-associated contrast improvement was accounted for by the combined effects of the near-threshold contrast pretest and the suprathreshold contrast exposure. We ran a control condition that contained only the near-threshold contrast discrimination pretest and the suprathreshold contrast exposure, but no training of near-threshold orientation discrimination. This control condition also contained any procedure learning that may also affect the cross-task transfer effects. Contrast threshold was improved by 12.5% ± 4.9% ($p = 0.016$, Figure 2c), which was not significantly different from the contrast threshold improvement after TPE training in Figure 2b ($p = 0.39$, two-tailed unpaired t test; Cohen's $d = 0.42$). Here the TI = 0.37 ± 0.16 when the mean contrast threshold improvement was normalized by the mean total improvement of contrast threshold in Figure 2b. These results thus do not support the possibility that the initial contrast threshold improvement after TPE training was a result of cross-task transfer from near-threshold orientation discrimination learning.

Experiment 2: The cross-task learning transfer from contrast discrimination to orientation discrimination

In Zhang et al. (2010) we also showed that near-threshold contrast discrimination learning did not transfer to a near-threshold orientation discrimination task either. Again with similar TPE training to that in Experiment 1, a new group of observers now practiced near-threshold contrast discrimination (Figure 3a). They also performed suprathreshold orientation discrimination in the same sessions to receive exposure to the orientation discrimination task. After this TPE training, the contrast threshold was improved by 26.0% ± 6.7% ($p = 0.008$, Figure 3b), and orientation threshold was improved by 14.4% ± 5.4% ($p = 0.013$, Figure 3b). The accuracy of suprathreshold orientation discrimination remained largely unchanged from 97.8% to 98.7%. The same observers then practiced near-threshold orientation discrimination, which further improved orientation threshold by 18.0% ± 5.4% relative to the previous TPE training effect (S13 vs. S7; $p = 0.014$, Figure 3b), for a total improvement of 32.4% ± 5.4% (S13 vs. S1). Here TI = 0.39 ± 0.13, which was significantly different from TI = 0 ($p = 0.016$) and from TI = 1 ($p = 0.002$), indicating potential partial learning transfer.

However, the orientation threshold improvement after TPE training was also accounted for by the combined effects of near-threshold orientation pretest and suprathreshold orientation exposure. In a control experiment that contained near-threshold orientation pretest and suprathreshold orientation exposure, but no near-threshold contrast discrimination training, orientation threshold was improved by 19.5% ± 6.0% ($p = 0.009$; Figure 3c), which was not significantly different from the initial improvement of orientation threshold after TPE training in Figure 3b ($p = 0.54$, two-tailed unpaired t test; Cohen's $d = -0.35$). Here TI = 0.60 ± 0.20 when the mean orientation threshold improvement was normalized by the mean total improvement of orientation threshold in Figure 3b. These results thus do not support the possibility that the initial orientation threshold improvement after TPE training was a result of cross-task transfer from near-threshold contrast discrimination learning.

In this and the previous experiments, the null differences between the threshold improvements after TPE training and the control condition may not be

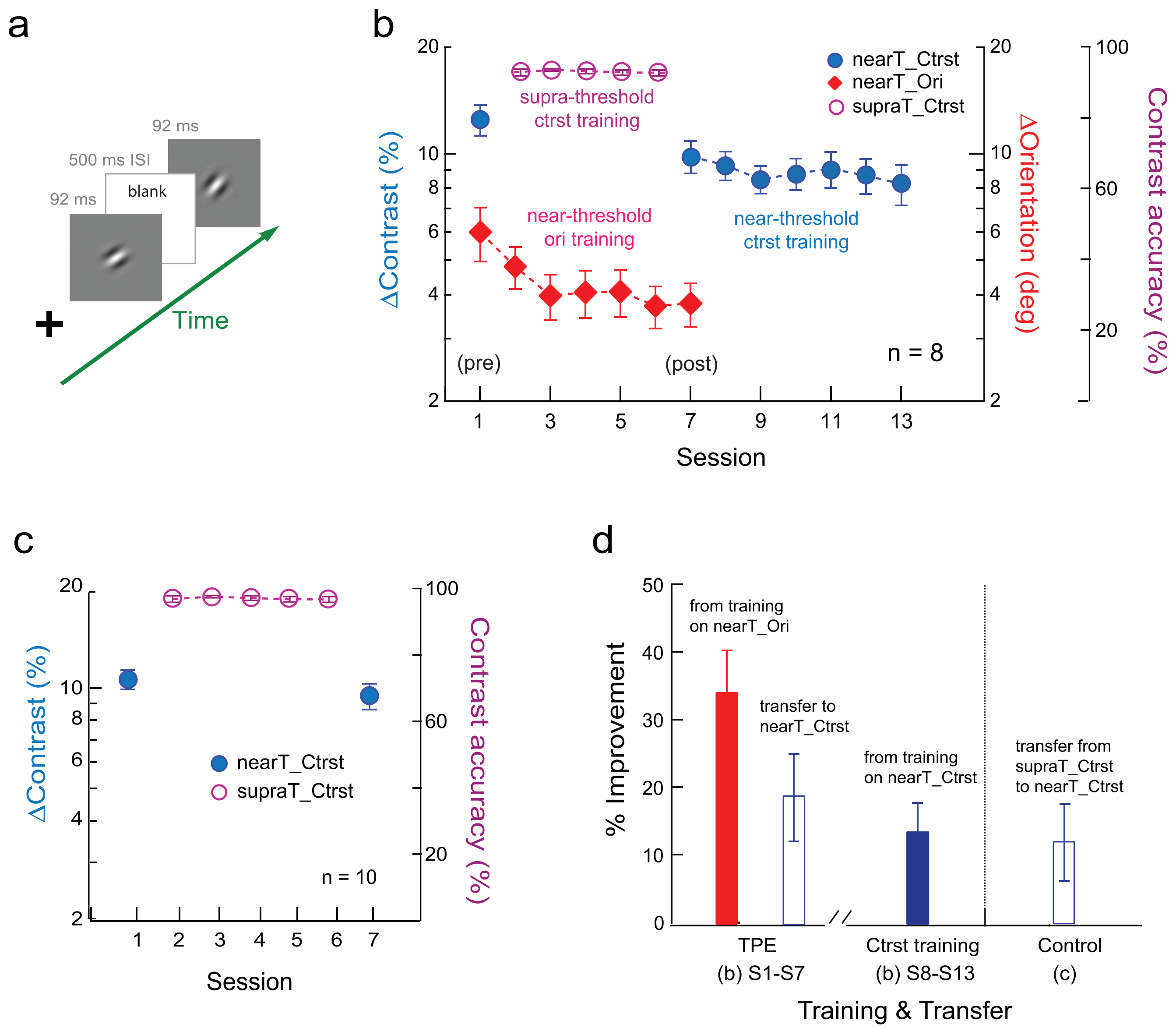

Figure 2. The effects of TPE training on the transfer of near-threshold orientation discrimination learning to near-threshold contrast discrimination. (a) Stimuli in an orientation discrimination trial. (b) The effects of TPE training on the transfer of near-threshold orientation discrimination learning (nearT_Ori; orientation thresholds indicated by the right ordinate; Symbols and relevant ordinate labels share the same color in Figures 2 and 3) to near-threshold contrast discrimination (nearT_Ctrst; contrast thresholds indicated by the left ordinate). The change of contrast threshold from S1 to S7 indicates the combined effects of near-threshold orientation training, near-threshold contrast pretest, and suprathreshold contrast exposure (supraT_Ctrst). Near-threshold contrast discrimination was further directly trained from S8 to S13. Error bars indicate ± 1 standard error of the mean. ΔContrast and ΔOrientation are the threshold-level stimulus differences between the two intervals in a 2IFC trial. (c) Control: The combined effects of near-threshold contrast pretest and suprathreshold contrast exposure, as well as any potential procedure learning, on contrast discrimination threshold. (d) A summary of learning and transfer in (b) and (c). From left: The first two bars indicate the amounts of near-threshold orientation discrimination learning and its transfer to near-threshold contrast discrimination, respectively, after TPE training. The third bar indicates further improvement of near-threshold contrast discrimination through training. The percentage improvement is relative to S7 thresholds. The fourth bar indicates improvement of near-threshold contrast discrimination due to suprathreshold contrast discrimination training in the control condition.

very much affected by the limited sample sizes, often a concern with perceptual learning studies. Here the group mean differences between the TPE conditions and the controls are small and opposite in trends in two experiments. Therefore increasing the sample sizes may not affect the effect sizes very much when the opposite trends between the TPE and control conditions are considered together. In contrast, previously

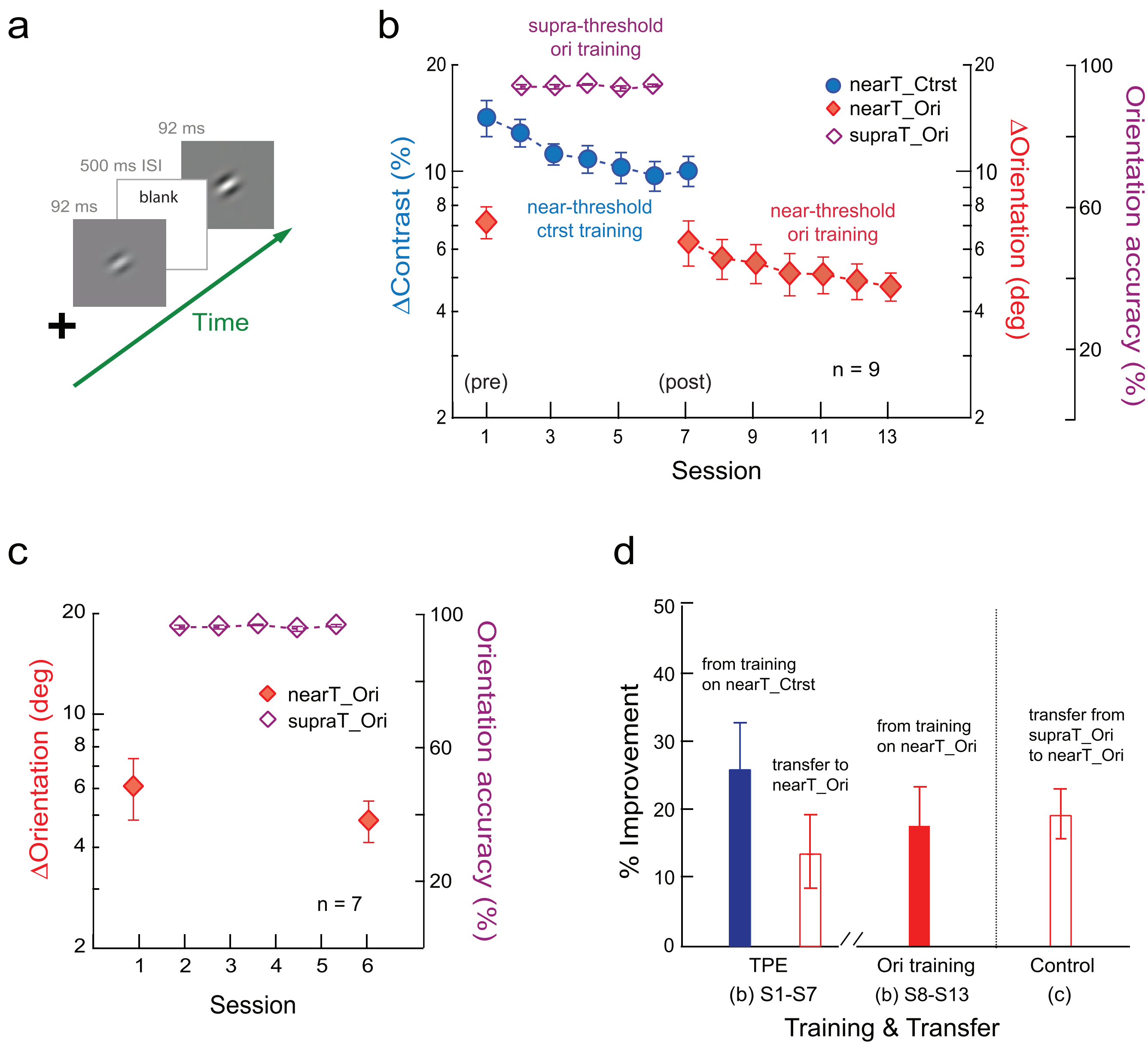

Figure 3. The effects of TPE training on the transfer of near-threshold contrast discrimination learning to near-threshold orientation discrimination with TPE training. (a) Stimuli in a contrast discrimination trial. (b) The effects of TPE training on transfer of near-threshold contrast discrimination learning (nearT_Ctrst; contrast thresholds indicated by the left ordinate) to orientation discrimination (nearT_Ori; orientation thresholds indicated by the right ordinate). The change of orientation threshold from S1 to S7 indicates the combined effects of near-threshold contrast discrimination training, near-threshold orientation pretest, and suprathreshold orientation exposure (supraT_Ori). Near-threshold orientation discrimination was further directly trained from S8 to S13. (c) Control: The combined effects of near-threshold orientation pretest and suprathreshold orientation exposure, as well as any potential procedure learning, on orientation discrimination threshold. (d) A summary of learning and transfer in (b) and (c). From left: The first two bars indicate the amounts of near-threshold contrast discrimination learning and its transfer to near-threshold orientation discrimination, respectively, after TPE training. The third bar indicates further improvement of near-threshold orientation discrimination through training. The improvement is relative to S7 thresholds. The fourth bar indicates improvement of near-threshold orientation discrimination due to suprathreshold orientation discrimination training in the control condition.

Zhang et al. (2010) found significant contrast learning transfer to an orthogonal orientation with TPE training (their figure 2). This finding excluded the control effects and involved fewer numbers of observers (six with TPE vs. five with control) but the effect size was larger (Cohen's $d = 1.50$). Thus, the current sample sizes are able to reveal TPE effects if these effects are robust.

Discussion

In this study we show that perceptual learning of near-threshold discrimination of two basic visual features, contrast and orientation, remains task specific even with TPE training. Our results thus fail to reveal a hypothetical general learning component in perceptual learning of basic visual features. These results are consistent with the existing observations of task specificity in perceptual learning (Ahissar & Hochstein, 1997; Crist, Kapadia, Westheimer, & Gilbert, 1997; Saffell & Matthews, 2003; Shiu & Pashler, 1992; Zhang et al., 2010).

The explanation of task specificity differs across different perceptual learning models. When learning is assumed to occur in retinotopic and feature selective early visual areas (Bejjanki, Beck, Lu, & Pouget, 2011; Karni & Sagi, 1991; Schoups et al., 1995; Teich & Qian, 2003), attentional modulation by training has to be invoked to explain why training of different tasks could lead to changes of different feature-tuning functions in the same neurons (Ahissar & Hochstein, 1993; Shiu & Pashler, 1992). Alternatively, in the context of re-weighting theories (Dosher & Lu, 1999; Law & Gold, 2009; Mollon & Danilova, 1996; Poggio, Fahle, & Edelman, 1992; Yu et al., 2004), the decision mechanisms learn to reweight task-related responses of visual neurons (e.g., orientation or contrast responses), which also leads to task specificity.

We postulate that task specificity results from the possibility that observers learn a specific set of rules for accomplishing a specific task in perceptual learning. We have demonstrated that location and orientation/direction specificity in perceptual learning can be substantially reduced or even eliminated with double training and TPE training (e.g., Xiao et al., 2008; Zhang et al., 2010; Zhang & Yang, 2014). These results indicate that perceptual learning may not only occur in more central brain areas as Mollon and Danilova (1996) once conjectured, but also be a rule-based cognitive process that allows learning transfer to untrained retinal locations and feature dimensions. We suggest that what is learned in perceptual learning are the rules for reweighting sensory inputs for performing the trained task, regardless of the stimulus location and orientation/direction (Zhang et al., 2010; Zhang & Yang, 2014). Therefore, different rules would be learned through practice of different stimulus features, which naturally leads to task specificity. The current results, which show no evidence for a general learning component, further constrain this understanding. They also set the boundary of the new double training and TPE methods in enabling the transfer of perceptual learning.

Under certain circumstances perceptual learning may transfer to other untrained tasks. For example, McGovern, Webb, and Peirce (2012) reported that for a group of Gabor stimuli, learning can more or less transfer among orientation, curvature, and global-form discrimination tasks depending on the relative complexity of the stimuli. However, these tasks all rely on orientation processing to some degree, which is different from traditional basic feature learning tasks that are independent from each other even if the stimuli are identical. Moreover, in the same study perceptual learning of these orientation-related tasks did not transfer to a contrast discrimination task using the same stimuli, which conforms to the rule of task specificity in perceptual learning.

In a recent study that also concerns cross-task training effects, Szpiro, Wright, and Carrasco (2014) limited the number of trials in an orientation learning task such that learning was not produced. They found that adding extra trials for a contrast discrimination task at the same orientation, which were insufficient to produce contrast discrimination learning either, could now enable significant orientation learning. Szpiro et al. (2014) suggested that their cross-task training effects are inconsistent with rule-based learning since the rules are different in two tasks. This study followed an earlier auditory learning study that also tested the cross-task training effects (Wright, Sabin, Zhang, Marrone, & Fitzgerald, 2010). Note that in the auditory study, tone frequency discrimination learning was enabled by additional exposure to the same tone frequency, i.e., the sound was played while the participants were performing a written symbol-to-number matching task. Therefore, additional experiments are needed to test whether the same exposure effects without training are applicable to visual learning.

It is noteworthy that we are unable to exclude the possibility that perceptual learning could eventually transfer among basic visual features when a new experimental design is invented in the future. Therefore, the concept of task specificity, even in the context of TPE training, needs to be taken with caution. For many years perceptual learning researchers have taken the failure of learning transfer to a new retinal location or feature dimension as evidence for location and feature specificity. However, most of them have overlooked a second possibility that learning is actually transferrable, but the transfer is impeded by other unknown processes. It is only after the double training and TPE findings that it became apparent that this second possibility is truer (Xiao et al., 2008; Zhang et al., 2010).

Finally we like to clarify a technical issue: During TPE training the near-threshold trials for the learning task and suprathreshold trials for the transfer task are mixed, which failed to improve the near-threshold

discrimination with the transfer task. This scenario is different from previous reports in which a mix of hard and easy trials of the same task would improve the task performance (e.g., Ahissar & Hochstein, 1997). In the same task training case, the easy trials provide information of the stimulus template to facilitate learning with hard trials. However, in the current TPE case the stimulus template information from easy trials are irrelevant to the trials of a different task.

Keywords: perceptual learning, task specificity, orientation, contrast

Acknowledgments

This research was supported by Natural Science Foundation of China grants 31230030 (CY) and 31470975 (JYZ).

*LJC and RJW contributed equally to this article.
Commercial relationships: none.
Corresponding authors: Jun-Yun Zhang; Cong Yu.
Email: zhangjunyun@pku.edu.cn; yucong@pku.edu.cn.
Address: Department of Psychology, Peking University, Beijing, China.

References

Ahissar, M., & Hochstein, S. (1993). Attentional control of early perceptual learning. *Proceedings of the National Academy of Sciences, USA*, *90*(12), 5718–5722.

Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, *387*(6631), 401–406.

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

Bejjanki, V. R., Beck, J. M., Lu, Z. L., & Pouget, A. (2011). Perceptual learning as improved probabilistic inference in early sensory areas. *Nature Neuroscience*, *14*(5), 642–648.

Crist, R. E., Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1997). Perceptual learning of spatial localization: Specificity for orientation, position, and context. *Journal of Neurophysiology*, *78*(6), 2889–2894.

Dosher, B. A., & Lu, Z. L. (1999). Mechanisms of perceptual learning. *Vision Research*, *39*(19), 3197–3221.

Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, *287*, 43–44.

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

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences, USA*, *88*(11), 4966–4970.

Law, C. T., & Gold, J. I. (2009). Reinforcement learning can account for associative and perceptual learning on a visual-decision task. *Nature Neuroscience*, *12*(5), 655–663.

Mastropasqua, T., Galliussi, J., Pascucci, D., & Turatto, M. (2015). Location transfer of perceptual learning: passive stimulation and double training. *Vision Research*, *108*, 93–102.

McGovern, D. P., Webb, B. S., & Peirce, J. W. (2012). Transfer of perceptual learning between different visual tasks. *Journal of Vision*, *12*(11):4, 1–11, doi: 10.1167/12.11.4. [PubMed] [Article]

Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, *10*(1), 51–58.

Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science*, *256*(5059), 1018–1021.

Saffell, T., & Matthews, N. (2003). Task-specific perceptual learning on speed and direction discrimination. *Vision Research*, *43*(12), 1365–1374.

Schoups, A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology*, *483*(Pt 3), 797–810.

Shiu, L. P., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception & Psychophysics*, *52*(5), 582–588.

Szpiro, S. F., Wright, B. A., & Carrasco, M. (2014). Learning one task by interleaving practice with another task. *Vision Research*, *101*, 118–124.

Teich, A. F., & Qian, N. (2003). Learning and adaptation in a recurrent model of V1 orientation selectivity. *Journal of Neurophysiology*, *89*(4), 2086–2100.

Wang, R., Cong, L. J., & Yu, C. (2013). The classical

TDT perceptual learning is mostly temporal learning. *Journal of Vision*, *13*(5):9, 1–9, doi:10.1167/13.5.9. [PubMed] [Article]

Wang, R., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2012). Task relevancy and demand modulate double-training enabled transfer of perceptual learning. *Vision Research*, *61*, 33–38.

Wang, R., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2014). Vernier perceptual learning transfers to completely untrained retinal locations after double training: A "piggybacking" effect. *Journal of Vision*, *14*(13):12, 1–12, doi:10.1167/14.13.12. [PubMed] [Article]

Wright, B. A., Sabin, A. T., Zhang, Y., Marrone, N., & Fitzgerald, M. B. (2010). Enhancing perceptual learning by combining practice with periods of additional sensory stimulation. *Journal of Neuroscience*, *30*(38), 12868–12877.

Xiao, L. Q., Zhang, J. Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology*, *18*(24), 1922–1926.

Xiong, Y. Z., Zhang, J. Y., & Yu, C. (2015). Understimulation at untrained orientation may explain orientation specificity in perceptual learning. *Journal of Vision*, *15*(12): 38, doi:10.1167/15.12.38. [PubMed] [Article]

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, *4*(3):4, 169–182, doi:10.1167/4.3.4. [PubMed] [Article]

Yu, C., Xiong, Y. Z., & Zhang, J. Y. (2015). Understimulation at untrained retinal locations may explain location specificity in perceptual learning. *Journal of Vision*, *15*(12): 1298, doi:10.1167/15.12.1298. [Abstract]

Zhang, J. Y., Cong, L. J., Klein, S. A., Levi, D. M., & Yu, C. (2014). Perceptual learning improves adult amblyopic vision through rule-based cognitive compensation. *Investigative Ophthalmology & Visual Science*, *55*(4), 2020–2030. [PubMed] [Article]

Zhang, J. Y., & Yang, Y. X. (2014). Perception learning of motion direction discrimination transfers to an opposite direction with TPE training. *Vision Research*, *99*, 93–98.

Zhang, J. Y., Zhang, G. L., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *Journal of Neuroscience*, *30*(37), 12323–12328.