Limited transfer of long-term motion perceptual learning with double training

Ju Liang School of Life Sciences, University of Science and Technology of China, Hefei, China

Yifeng Zhou School of Life Sciences, University of Science and Technology of China, Hefei, China

Manfred Fahle University of Bremen, Center for Cognitive Sciences, Bremen, Germany

Zili Liu Department of Psychology, University of California, Los Angeles, USA

A significant recent development in visual perceptual learning research is the double training technique. With this technique, Xiao, Zhang, Wang, Klein, Levi, and Yu (2008) have found complete transfer in tasks that had previously been shown to be stimulus specific. The significance of this finding is that this technique has since been successful in all tasks tested, including motion direction discrimination. Here, we investigated whether or not this technique could generalize to longer-term learning, using the method of constant stimuli. Our task was learning to discriminate motion directions of random dots. The second leg of training was contrast discrimination along a new average direction of the same moving dots. We found that, although exposure of moving dots along a new direction facilitated motion direction discrimination, this partial transfer was far from complete. We conclude that, although perceptual learning is transferrable under certain conditions, stimulus specificity also remains an inherent characteristic of motion perceptual learning.

Introduction

Visual perceptual learning is defined as the visual system's capability to improve signal detection, discrimination, or identification in optical stimuli via practice (Epstein, 1967; Fahle & Poggio, 2002; Gibson, 1969; Sagi, 2011). For example, in a motion perceptual learning task, two motion stimuli are sequentially shown (Figure 1). In each stimulus, random dots move along a single direction. From the first stimulus to the second, the motion direction changes either 0° or 3°. Participants decide whether or not the two directions were the same. Under such conditions, Ball and Sekuler (1982, 1987) found that participants substantially improved this direction discrimination through training. They also found that the improvement did not transfer to an untrained average direction that was 90° or more from the trained average direction.

Until the mid-1990s, it was believed that humans could improve in almost any visual perceptual task, but could not transfer the learning from the trained stimulus attribute t o a new attribute, e.g., from the trained direction to a new direction (Fahle, 1997; Fiorentini & Berardi, 1981; Gilbert, 1994; Karni & Sagi, 1991; O'Toole & Kersten, 1992; Ramachandran & Braddick, 1976). Three studies in the mid-1990s, however, challenged the notion that perceptual learning could not transfer (Ahissar & Hochstein, 1997; Liu, 1995; Rubin, Nakayama, & Shapley, 1997) (see also Gibbs, 1951; Lordahl & Archer, 1958). These studies indicated that when task difficulty was reduced, learning could transfer to other stimulus attributes. Specifically, in a motion direction discrimination task (Figure 1), Liu (1995, 1999) enlarged the directional difference from 4° to 8° and found that learning transferred to untrained directions. Ahissar and Hochstein (1997), in a visual search task with oriented bars, manipulated either the possible locations of the target bar or the angular difference between the target bar and background bars. In both cases, they found that training with an easier task transferred when the orientations of the target and background bars were

Citation: Liang, J., Zhou, Y., Fahle, M., & Liu, Z. (2015). Limited transfer of long-term motion perceptual learning with double training. *Journal of Vision*, *15*(10):1, 1–9, doi:10.1167/15.10.1.

doi: 10.1167/15.10.1 Received January 2, 2015; published July XX, 2015 ISSN 1534-7362 © 2015 ARVO

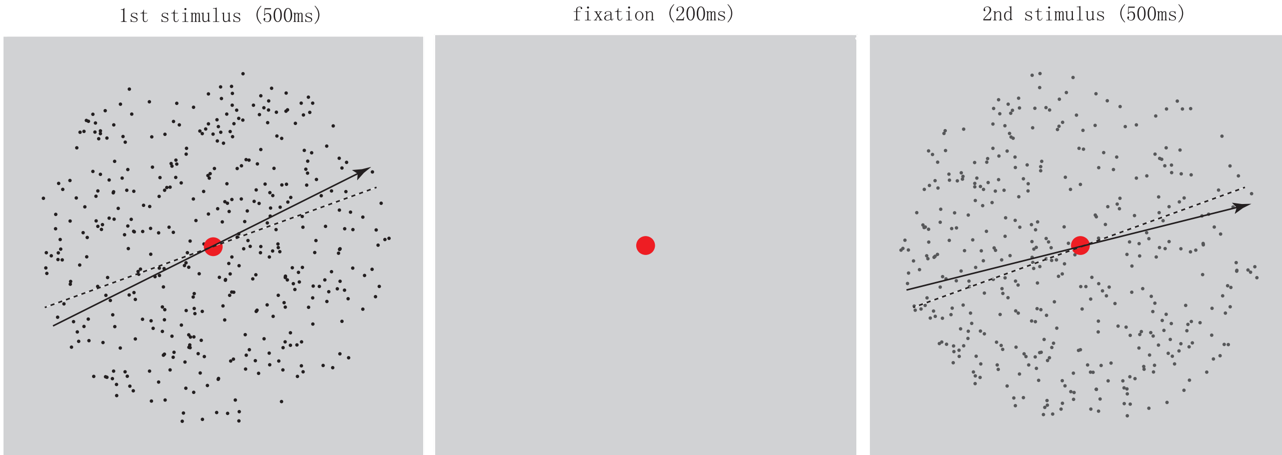

Figure 1. Schematic illustration of a motion direction discrimination trial, adapted from Ball and Sekuler (1982, 1987). The circular aperture remained stationary while the dots inside moved in a single direction in each stimulus. The participant fixated at the central red disk and decided whether the motion directions of the two stimuli were the same or different.

swapped. In Rubin et al.'s shape discrimination task (1997), inclusion of easier-to-discriminate shapes enabled improved discrimination of harder-to-discriminate shapes.

More recently, Xiao et al. (2008) reported a double training technique that gave rise to complete transfer in all tasks that had been tested, including motion direction discrimination (Zhang et al., 2010; Zhang & Yang, 2014). For example, Zhang and Yang (2014) used in their first leg of training a motion direction discrimination task. In their second leg of training, they used a discrimination task of dot numbers between two motion stimuli, which moved along a new average direction. After the second leg of training, Zhang and Yang (2014) found that motion direction discrimination transferred completely from the first to the second leg's direction.

This double training technique and the associated results are significant because they imply that stimulus specificity, the trademark finding in decades of research on perceptual learning, may not be as important as previously thought. If the transfer is substantial, the argument goes, then perceptual learning is hardly different from other types of learning. These other types of learning typically use more complex stimuli and give rise to much less specificity as compared to when simpler perceptual features are used for learning (Fine & Jacobs, 2002; Green & Bavelier, 2003). Indeed, the Zhang et al. (2010) study was entitled "Rule-based learning explains visual perceptual learning and its specificity and transfer." If confirmed, the field of visual perceptual learning will face a major shift.

We, however, observed the following. In all prior studies using the double training technique, training never exceeded seven sessions in each leg. Although seven training sessions were not uncommon in perceptual learning studies, there were also studies with many more training sessions (Poggio, Fahle, & Edelman, 1992; Liu & Weinshall, 2000). In addition, Jeter, Dosher, Liu, and Lu (2010) found that, in an orientation discrimination task, long-term training tended to lead to specificity, whereas short-term learning tended to lead to substantial transfer. It is important therefore to ascertain whether the double training technique applies to longer-term training.

Why is it important to study longer-term training? Because there is evidence in the literature that there was a fast learning phase associated with shorter-term training, and a slow learning phase associated with longer-term training in hyper acuity learning (Poggio, Fahle, & Edelman, 1992). In addition, it is common in perceptual learning studies that participants practice the task before data are collected. This is because of the inevitable general task learning that is likely different from perceptual learning, and may be easier to transfer from one stimulus attribute to another. Although this practice helps reduce the influence from the general learning, it is unknown how much practice can completely remove this influence. We are not suggesting here that the fast learning or any study using the double training technique was confounded by general learning. Our point is that, with longer-term training, any effect of general learning is further diminished and that the learning is more likely to be perceptual. In this sense, with longer-term and double training, if learning is again found to completely transfer, it will be stronger evidence that the double training technique applies to an even wider range of tasks, stimuli, and experimental methods. In the current study, we tested this hypothesis by using motion direction discrimination in the first leg of task, and contrast discrimination of moving dots in the second leg of task.

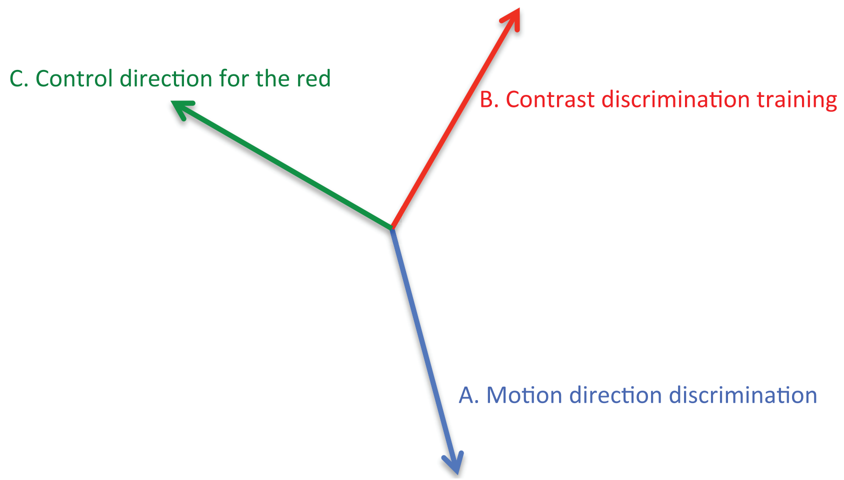

Figure 2. Schematic illustration of the experimental design. The blue direction served as the first average training direction of motion direction discrimination. The red direction served as the second training direction of contrast discrimination. The green direction served as the control direction. The contrast-trained (red) and control (green) directions were perpendicular to each other, symmetric about the motion-trained (blue) direction, and counterbalanced between participants. In the experiment, all three directions were oblique.

Experiment

Methods

The stimuli and task were similar to those used in Ball and Sekuler (1982, 1987), Liu and Weinshall (2000), and Wang, Zhou, and Liu (2013), except that the dots were darker than the background. Specifically, 400 dots were randomly distributed within a circular aperture of 8° in diameter (262 pixels; Figure 1). Each dot was 0.09° × 0.09° in visual angle (3 × 3 pixels). In each of the two stimuli per trial, all dots moved along a single direction, with a speed of 10°/s. The duration of each stimulus was 500 ms, and the interstimulus interval was 200 ms. Motion directions of the two stimuli always differed by +3° or −3°. As an example, the two directions were either 73.5° and 76.5°, or 76.5° and 73.5°. The luminance of the dots in the first stimulus also always differed from the second. One luminance value was 7.2 cd/m^2, and the other was 9.2 cd/m^2, with random assignment. The background luminance was 57.1 cd/m^2. In the motion direction discrimination task, the participant fixated at a central red disk and decided which of the two intervals contained a more clockwise motion direction. In the contrast discrimination task, the participant also fixated at the central disk and decided which interval was darker. The central fixation disk had a diameter of 0.5° (16 pixels) and a luminance of 16.5 cd/m^2. Trialwise feedback was provided by a computer beep.

Two triplets of average motion directions were chosen: (A = 75°, B = 210°, C = 300°) and (A = 285°, B = 150°, C = 60°; Figure 2). Within each triplet, the A direction was chosen as the first average direction for motion direction discrimination training. The remaining two directions were perpendicular to each other and symmetric about the first direction. One of these two directions served as the second leg direction for contrast discrimination training, the third direction served as the control direction for the second direction (counterbalanced between participants). All directions were deliberately chosen to be oblique. The main experimental procedure was as follows.

(1) Motion direction discrimination training. After the baseline performance had been measured in motion direction discrimination and contrast discrimination along all directions in two daily sessions, participants were trained along the A direction with 21 sessions, each with 720 trials. (Some participants were also tested with their motion discrimination along the B, C directions during training.) At the end of this training, motion direction along the B and C directions and contrast discrimination along all three directions were measured.

(2) The second leg of training. The participants were trained with contrast discrimination of dots along the B direction for 21 sessions, each again with 720 trials. The stimuli were identical as in the direction discrimination training, except that the average direction was changed. During training, direction discrimination along the B and C directions was also assessed.

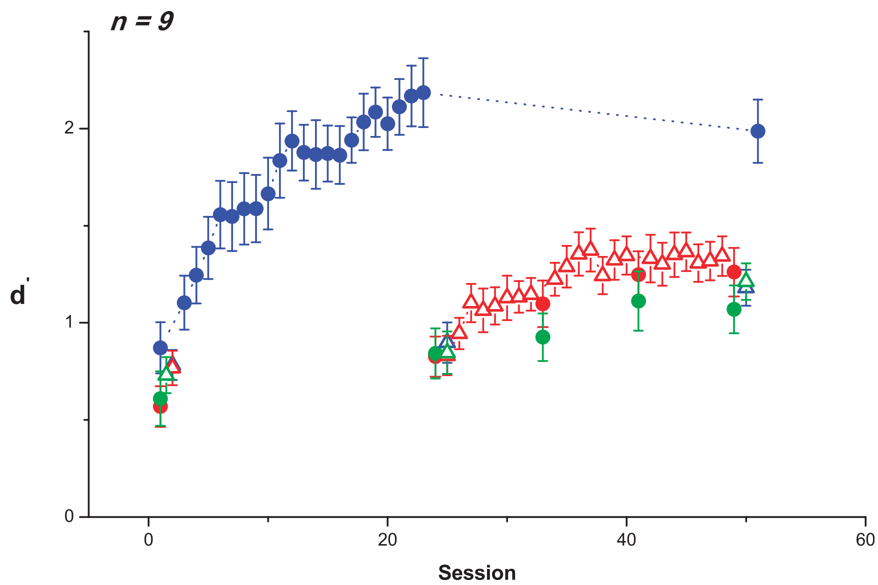

Figure 3. Group averages where data from all nine participants were available. The circular symbols represent motion discrimination performance, and the triangular symbols represent contrast discrimination performance. The blue color represents the motion-trained direction, the red color represents the contrast-trained direction, and the green color represents the control direction. The error bars represent standard errors of the mean (same as in Figures below). During the first leg of training, motion direction discrimination was assessed along the contrast-to-be-trained (red) and control (green) directions for some, but not all, participants. These data are not shown here, but will be shown in the individual participant's data plot below.

(3) Transfer measurement. Direction discrimination and contrast discrimination along all three directions was assessed at the end.

Nine students from the University of Science and Technology of China, Hefei, participated. The recruitment adhered to the Declaration of Helsinki.

A 17-inch Sony Multiscan G220 computer monitor (Sony, Ichinomiya, Aichi, Japan) was used. The resolution was 1024 × 768 pixels, and the refresh rate was 100 Hz. The participants viewed the stimuli binocularly from a chin rest. The viewing distance was 60 cm. The experiment used the MatLab software (Mathworks, Inc., Natick, MA) and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Results and discussion

In the first leg of direction discrimination training, the average improvement in d′ was 1.31 along the trained direction, and 0.24 along the two untrained directions, demonstrating direction specific learning, $t(8) = 7.50$, $p = 0.0001$, two-tailed (same below). The average transfer from the trained to the untrained directions was 18%, far below the 100% required for complete transfer. This result was consistent with the traditional data in the literature of learning specificity (see Fahle, 2005, and Sagi, 2011 for reviews). Figures 3 and 4 show all the data.

Contrast to motion discrimination transfer

After 21 sessions of contrast discrimination training, the improvement in d' in *motion discrimination* was 0.43 along the contrast-trained (red, B) direction, and was 0.23 along the control (green, C) direction. This difference was statistically significant, $t(8) = 3.42$, $p = 0.009$. It indicates that exposure to the motion stimuli, even in a task irrelevant to motion, facilitated subsequent motion direction discrimination, concurring qualitatively with Xiao et al. (2008) and Zhang and Yang (2014). Quantitatively, however, this improvement due to exposure of motion stimuli (0.43 in d′) was only 36% of the average improvement in the first leg (1.31), substantially smaller than the complete transfer as reported in Xiao et al. (2008) and Zhang and Yang (2014; the improvement along the control direction was 17%). Our result indicates the task specific nature of motion direction discrimination learning. Namely, if the training task was not motion direction discrimination, it was much less effective in improving motion direction discrimination, *even though* motion direction discrimination had already been trained for 21 sessions along a different direction.

It should be emphasized that the lack of complete transfer was not just a result from averaged data, it held for every single participant of the nine total participants. An additional way to illustrate this is to look at the motion discrimination data along all three directions at the very end (Figures 3 and 4). If one is willing to ignore any small differences in motion discrimina-

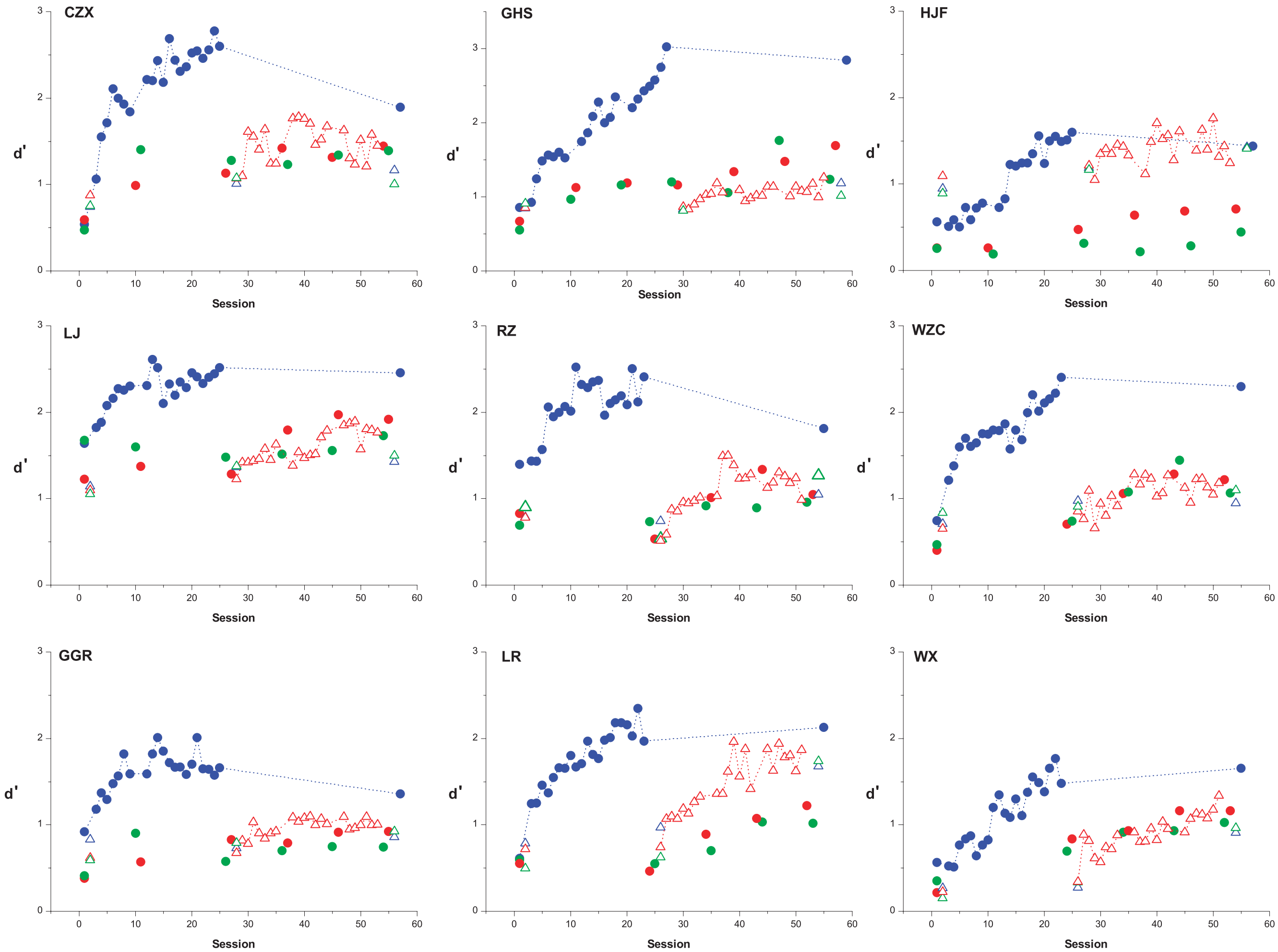

Figure 4. Each of the nine individual trainees' data. Participant JL is the first author. It is noteworthy that no participant completely (100%) transferred motion discrimination to the contrast-trained direction at the end. Meanwhile, the contrast-trained (red) direction showed numerically better performance than the control (green) direction, for every trainee. That is, at the end of every plot, the blue dot (motion-trained direction) is higher than the red (contrast-trained direction), which in turn is higher than the green (control direction).

tion between these directions at the very beginning, one can readily see that the final performance along the motion-trained direction (blue) was higher than along either of the other two directions (contrast trained [red] and control [green]).

The motion discrimination d′ decreased ($\Delta d' = -0.20$) from the beginning to the end of the second leg of training in contrast discrimination. Even after this decrease was taken into consideration and transfer recalculated accordingly, the amount of transfer in motion discrimination along the second leg, contrast-trained (red) direction (0.43) was 46% of the first leg improvement (1.12).

Motion to contrast discrimination transfer

We also looked at any possible transfer in the opposite direction, from motion discrimination to contrast discrimination. After all, the stimuli used in the two legs of training were identical. In the first leg of training in motion discrimination, *contrast discrimination* along the motion-trained direction improved only by 0.10 in d′, $t(8) = 2.11$, $p = 0.07$. In the second leg of training, contrast discrimination along the contrast-trained direction improved by 0.51, which was significantly greater than that along the motion-trained direction in the first leg of training, $t(8) = 3.00$, $p = 0.02$. This indicates task specificity of training. Also in the second leg, the improvement of contrast discrimination along the trained direction (0.51) was more than along the other two directions (0.32) ($t[8] = 2.68$, $p = 0.03$). This indicates stimulus specific learning (the training stimuli moved along a specific average direction).

Of the two untrained directions in the second leg, one was the control (green) direction ($\Delta d' = 0.37$), the other was the motion-trained (blue) direction in the first leg ($\Delta d' = 0.28$). The difference between these two directions in contrast discrimination was not significant, $t(8) = -1.13$, $p = 0.28$. This null result is consistent with the finding in Xiao et al. (2008). Namely, exposure (to the motion-trained direction A) before training (in direction B of contrast discrimination) facilitated little transfer of contrast learning from the B direction to the A direction. In Xiao et al. (2008), the (second leg of) exposure had to be after the first leg of training.

In a pilot study before our pretests, we adjusted the luminance difference of the dots between the two stimuli in a trial, in an attempt to equate the performance between the two tasks. It turned out that the pretest motion discrimination sensitivity was $d' = 0.68$, and the pretest contrast discrimination sensitivity was $d' = 0.76$. They were not statistically different ($t < 1$). Given the approximately equal performance at the beginning, the learning speed for motion discrimination ($\Delta d' = 1.31$ in 21 sessions) was apparently higher than for contrast discrimination ($\Delta d' = 0.51$ in 21 sessions) ($t[8] = 3.60$, $p = 0.01$). It remains unclear whether this speed difference was due to task difference or due to the fact that the motion training was before contrast training. But we do not believe that answering this question is critical in our hypothesis testing, because the main point of the second leg of training in Xiao et al. (2008) is exposure.

We also correlated the amount of learning between the first and second legs across participants, but no statistically reliable result was found ($r = -0.13$). At the end of the second leg of training, we also correlated the amount of motion learning in the first leg along the trained direction and the amount of motion transfer. The correlation between the motion-trained direction and the contrast-trained direction was low ($r = 0.16$) and nonsignificant ($t < 1$). Only the amount of motion learning between the contrast-trained direction B and the control direction C showed a moderate correlation, $r = 0.59$, $t(7) = 1.93$, $p < 0.05$. (The t test was one-tailed, since it should be reasonable to expect that the correlation is positive between the two transfer directions).

Figure 5 summarizes the main results by plotting the amount of d′ improvement in motion discrimination, along all three directions in each of the two legs of training. After the first leg of training in motion discrimination, the transfer to the other two directions was similar. This was expected because these two directions were symmetric about the training direction, and therefore should be equal after the first leg of training. After the second leg of training in contrast discrimination, the improvement along the contrast-trained direction was greater than along the control direction. This means that exposure of the motion stimuli along the contrast-trained direction facilitated transfer of motion discrimination. This facilitation was qualitatively consistent with Xiao et al. (2008), even though it did not give rise to full transfer.

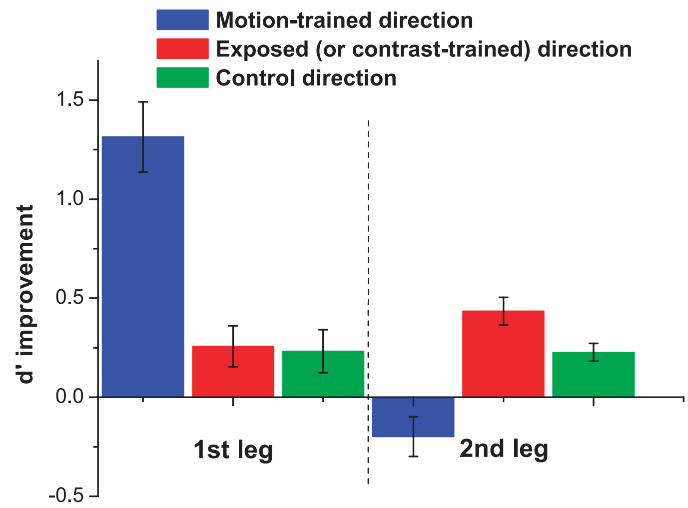

Figure 5. The amount of d′ improvement in motion discrimination along all three directions, and in the two legs of training. The improvement in the first leg of training was calculated by subtracting the pre-training d′ from the post-training d′ of the first leg. The improvement in the second leg was calculated by taking the difference between post- and pre-training d′ of the second leg.

General discussion and conclusions

Stimulus and task specificity have long been trademark characteristics of traditional visual perceptual learning. This specificity has been thought to reflect the receptive field properties of early stages of the visual system (Yan et al., 2014). On the other hand, if perceptual learning can transfer, there would be tremendous practical implications (Fahle, 2005b).

In light of this substantial importance of specificity versus transfer, the implication of the double training technique introduced by Xiao et al. (2008) and Zhang and Yang (2014) is highly significant. The significance is due to the claim by the double training studies that the specificity may not be an inherent property of perceptual learning, and that transfer could be readily obtained when participants were trained in a different and better way.

Our study was originally based on the observation that no studies with the double training technique had more than seven training sessions in either of the two training legs. Although it is not well understood whether learning within this timeframe of seven sessions is different from longer-term learning, it is known from the literature that longer-term training is commonplace and often gave rise to stimulus specificity. We therefore decided to test the double training technique in longer-term motion perceptual learning, and to use the method of constant stimuli.

Unfortunately, we could not find substantial transfer in our study. When this happened, it is necessary to carefully consider the differences between our study and earlier studies in the literature, particularly the Zhang and Yang (2014) study. Our study was different from the earlier studies with double training in the following aspects: (a) Our training of 21 sessions in each leg was much longer than that used in the double training in the literature. (b) We used the method of constant stimuli whereas the method of staircase (constant accuracy) had been used in all prior double training studies. (c) Our second leg, the exposure task, was contrast discrimination, whereas Zhang and Yang (2014) used a dot number discrimination task as their exposure task. (d) In Zhang and Yang (2014), the direction in the second leg of training was exactly opposite to the first leg of training direction. In our study, these two directions were 135° away from each other. (e) The precise stimulus luminance values in Zhang and Yang (2014) were neither reported nor available upon request. These values were different from ours, particularly since their dots had a constant luminance whereas our dots changed luminance between the two stimuli in a trial.

When no complete transfer could be found, any of these differences could be responsible, although some were more likely than others. For example, given that the purpose of the second leg task was to expose motion stimuli along a new direction, the exact task should be of little relevance. In comparison, our method of constant stimuli may turn out to make an important difference. Given that the directional difference in our motion discrimination was $\pm 3°$, the task was difficult. A relevant study in this respect is by Hung and Seitz (2014), who also used five training sessions with staircase as in Zhang and Yang (2014). However, instead of resetting to a high threshold at the beginning of each training session, they used a single staircase throughout the five training sessions. In effect, the stimulus was mostly at threshold, thereby providing less number of easier trials. Hung and Seitz (2014) argued that this was the main reason the double training in their Vernier discrimination task gave rise to much less transfer. Our own critique of this study is that there appeared only limited learning in the entire single staircase, with five sessions (figure 3B, page 8426). Given that threshold was obtained from the first 100 trials in each training session, the learning seemed to have occurred mainly from the first to second session. Because the first threshold was obtained from the very first 100 trials (or less if there were 20 reversals of the staircase before reaching the 100th trial), there might be practice effect confounded with the perceptual learning. Another concern regarding the amount of learning is that the participants' threshold changed from 7 to 4.5 arcmin, whereas in figure 1B a different group of participants learned from 11 to 6 arcmin. This means that the second group of participants could reach a post-learning threshold that was only 1 arcmin less than the pre-learning threshold of the first group of participants. Individual differences aside, the apparent lack of substantial learning may have weakened the authors' claim that the specificity was due to the single staircase training.

Another issue related to the method of constant stimuli vs. staircase is in regard to the way in which transfer was measured. Jeter, Dosher, Petrov, and Lu (2009) argued in an orientation discrimination study that the amount of transfer was determined by the difficulty of the task during transfer measurement, whereas the difficulty of the training task was irrelevant. In our task of motion discrimination, therefore, one might argue that since the task measuring transfer was difficult ($\pm 3°$), no transfer could be found. In comparison, when a staircase was used in measuring transfer that contained both difficult and easy trials, more transfer could be obtained. This argument, however, has the following two problems. The first is that Zhang and Yang (2014) in fact found specificity when their second leg of exposure task was not used, even though they used staircase to measure transfer. The second is that Wang, Zhou, and Liu (2013) found that, in motion discrimination learning, the amount of transfer indeed depended on the difficulty of the training task, and did not depend exclusively on the transfer task.

In light of these studies in the literature that addressed the issue of constant stimuli versus staircase, task difficulty, and training time, we have since studied the double training technique by first exactly replicating in method the original Zhang and Yang (2014) study with simultaneous training along the two average directions, and then extending the training time to 21 sessions. We have also started a shorter-term version of our current study. Namely, everything would be kept unchanged except that the number of training sessions would match that in Zhang and Yang (2014). These studies however are beyond the scope of the current study. We will report them separately.

Keywords: perceptual learning, motion discrimination, double training, long term, transfer, specificity.

Acknowledgments

This research was supported in part by a fellowship to ZL at the Hanse Institute of Advanced Studies (HWK), Delmenhorst, Germany; and by the National Natural Science Foundation of China to ZL (NSFC

31228009) and to YZ (NSFC 31230032). Correspondence should be sent either to ZL or YZ. We thank helpful discussion with Dr. Cong Yu. We also thank Dr. Nestor Matthews for helpful and critical discussion and English editing.

Commercial relationships: none.
Corresponding author: Zili Liu.
Email: zili@psych.ucla.edu.
Address: Department of Psychology, University of California, Los Angeles, USA.

References

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

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

Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research, 27*(6), 953–965.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Epstein, W. (1967). *Varieties of perceptual learning*. New York, St. Louis, San Francisco, Toronto, London, Sydney: McGraw-Hill Book Company.

Fahle, M. (1997). Specificity of learning curvature, orientation, and vernier discriminations. *Vision Research, 37,* 1885–1895.

Fahle, M. (2005). Perceptual learning: specificity versus generalization. *Current Opinion in Neurobiology, 15*(2), 154–160.

Fahle, M. (2005b). Learning to tell apples from oranges. *Trends in Cognitive Sciences, 9*(10), 455–457.

Fahle, M., & Poggio, T. (2002). *Perceptual learning*. Cambridge, MA; London, England: The MIT Press.

Fine, I., & Jacobs, R. A. (2002). Comparing perceptual learning tasks: a review. *Journal of Vision, 2*(2):5, 190–203, doi:10.1167/2.2.5. [PubMed] [Article]

Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research, 21,* 1149–1158.

Gibbs, C. B. (1951). Transfer of learning and skill assumptions in tracking tasks. *Quarterly Journal of Experimental Psychology, 3,* 99–110.

Gibson, E. J. (1969). *Principles of perceptual learning and development*. New York: Appleton-Century-Crofts, Educational Division, Meredith Corporation.

Gilbert, C. D. (1994). Early perceptual learning. *PNAS, USA, 91,* 1195–1197.

Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature, 423,* 534–537.

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

Jeter, P. E., Dosher, B.A., Petrov, A., & Lu, Z.-L. (2009). Task precision at transfer determines specificity of perceptual learning. *Journal of Vision, 9*(3):1, 1–13, doi:10.1167/9.3.1. [PubMed] [Article]

Jeter, P. E., Dosher, B.A., Liu, S.-H., & Lu, Z.-L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research, 50,* 1928–1940.

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *PNAS, USA, 88,* 4966–4970.

Liu, Z. (1995). *Learning a visual skill that generalizes*. (Princeton, NJ: NEC Research Institute.

Liu, Z. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. *PNAS, USA, 96,* 14085–14087.

Liu, Z., & Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research*, *40*(1), 97–109.

Lordahl, D. S., & Archer, E.J. (1958). Transfer effects on a rotary pursuit task as a function of first-task difficulty. *Journal of Experimental Psychology, 56,* 421–426.

O'Toole, A. J., & Kersten, D. (1992). Learning to see random-dot stereograms. *Perception, 21,* 227–243.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442.

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

Ramachandran, V. S., & Braddick, O. (1976). Orientation-specific learning in stereopsis. *Perception, 2,* 371–376.

Rubin, N., Nakayama, K., & Shapley, R. (1997). Abrupt learning and retinal size specificity in illusory-contour perception. *Current Biology*, *7*(7), 461–467.

Sagi, D. (2011). Perceptual learning in vision research. *Vision Research, 51,* 1552–1566.

Wang, X., Zhou, Y., & Liu, Z. (2013). Transfer in motion perceptual learning depends on the difficulty of the training task. *Journal of Vision, 13*(7):5, 1–9, doi:10.1167/13.7.5. [PubMed] [Article]

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.

Yan, Y., Rasch, M.J., Chen, M., Xiang, X., Huang, M., Wu, S., & Wu, L. (2014). Perceptual training continuously refines neuronal population codes in primary visual cortex. *Nature Neuroscience, 17,* 1380–1387.

Zhang, J. Y., & Yang, Y.X. (2014). Perceptual 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,* 12323–12328.