Specificity of motion discrimination learning even with double training and staircase

Ju Liang

Zili Liu

Yifeng Zhou

Manfred Fahle

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

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

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

Department of Psychology, University of California, Los Angeles, CA, USA

\sim
ואלו

 \searrow

Visual perceptual learning has been traditionally characterized by its specificity. Namely, learning transfers little to many untrained stimulus attributes. This result of specificity is the basis for the inference that perceptual learning takes place in low-level visual areas in the brain. Recently, however, Xiao and colleagues (2008) demonstrated a double training technique that enabled complete transfer of learning in all tasks that were tested. This technique has since been applied to motion direction discrimination learning. Learning along one average direction has been found to transfer completely to a new average direction, along which only dot number discrimination had been trained (J. Y. Zhang & Yang, 2014). In the current study, we first repeated the J.Y. Zhang and Yang (2014) experiment in exact procedure, stimuli, and task. We then continued the double training to examine transfer in longer-term perceptual learning. To our surprise, in both our exact replication attempt and in our longer-term learning study, we could not find complete transfer. In fact, the transfer to the dot number discrimination direction was no greater than to an untrained control direction. We suggest that individual differences and subtle differences in experimental setup between J. Y. Zhang and Yang (2014) and our studies are too strong and common to determine whether or not the new double training technique can bring about complete transfer in motion discrimination learning.

Introduction

One recent important development in perceptual learning research is the double training technique that

was first reported by Xiao et al. (2008). This publication is important because it showed that perceptual learning could completely transfer when prior studies found high specificity (Epstein, 1967; Fahle and Poggio, 2002; Gibson, 1969).

Specifically, Xiao et al. (2008) first replicated the conventional finding of stimulus-specific learning by training participants with a contrast discrimination task at the upper-left visual quadrant using vertical Gabors. They then tested the same task at the lowerright quadrant and found little transfer of learning. This confirmed the prior result that this contrast discrimination learning was retinal location specific. Xiao et al. (2008) then applied their double training technique, as follows. In alternating blocks, they trained a new group of participants with contrast discrimination at the upper-left quadrant using vertical Gabors and orientation discrimination at the lower-right quadrant using nearly horizontal Gabors. After this double training, transfer of contrast discrimination was tested at the lower-right quadrant using vertical Gabors. Complete transfer of learning was found.

This result is theoretically significant because stimulus specificity had remained as the signature characteristic in perceptual learning, despite prior studies demonstrating transfer of learning when task difficulty was manipulated (Ahissar and Hochstein, 1997; Liu, 1995, 1999; Rubin, Nakayama, & Shapley, 1997; for reviews, see Fahle, 2005 and Sagi, 2011). The result of stimulus specificity in the vast number of studies in the literature had been interpreted as

Citation: Liang, J., Zhou, Y., Fahle, M., & Liu, Z. (2015). Specificity of motion discrimination learning even with double training and staircase. *Journal of Vision*, 15(10):3, 1–9, doi:10.1167/15.10.3.

evidence that perceptual learning can take place at low stages of neural processing in the brain, because lowlevel neurons respond selectively to stimulus attributes. For example, perceptual learning of contrast discrimination had been found to be specific to retinal location and that of orientation discrimination had been found to be specific to the stimulus orientation (Crist, Kapadia, Westheimer, & Gilbert, 1997; Fahle, 1997; Saarinen & Levi, 1995). These results were taken as evidence that learning takes place in early vision because of a neuron's small receptive field at the primary visual cortex and the cortex's precise retinotopic organization.

In light of this background, Xiao et al.'s challenge in 2008 with their complete transfer results is fundamental. This is because, according to these authors, stimulus specificity was not necessarily an essential characteristic of perceptual learning but a by-product of training methods. If confirmed, perceptual learning as a field, with its core characteristic of stimulus specificity, will no longer be uniquely different from other kinds of learning, for example, language learning or concept learning.

Another reason that the challenge from Xiao et al. (2008) is significant is that their results apparently generalize across tasks and stimuli. Since the publication of Xiao et al. (2008), this double training technique has been applied, and complete transfer was found in all perceptual learning tasks and stimuli tested (J. Y. Zhang et al., 2010; T. Zhang, Xiao, Klein, Levi, & Yu, 2010). These included stimuli and tasks widely used in previous studies. Some of the results have also been independently verified (Hung & Seitz, 2014). This technique of double training has been further extended to visual motion perception. For example, J. Y. Zhang and Yang (2014) showed that when motion direction discrimination training along an average direction was accompanied by training with dot number discrimination along the opposite direction, complete transfer of motion discrimination was achieved from the motion trained to the dot number trained direction.

Because of the theoretical significance of this double training technique and of the empirical results found in a wide range of tasks, we decided to independently replicate some of the studies. The task we chose was motion direction discrimination learning, a topic we were relatively familiar with. Here, we asked two specific questions.

- 1. How robust is the complete transfer result in J. Y. Zhang and Yang (2014)? To address this question, we replicated their experiment exactly, to the extent that we also used exactly the same computer program.
- 2. We observed that in all studies using the double training technique, the total number of sessions was

never more than eight. We asked whether complete transfer could still be found with much longer training.

To anticipate, our attempted replications in two separate laboratories could not find complete transfer. In fact, to our surprise, exposure of moving dots along an average direction in the dot number discrimination task facilitated little subsequent motion direction discrimination along that direction. Neither additional training nor exposure facilitated motion transfer.

Experiment 1 in China

Methods

There were two stages in our experiment. The first stage replicated all possible details of the original experiment (experiment 2; J. Y. Zhang & Yang, 2014), with the computer program kindly provided by Zhang. The second stage was a continuation beyond the original study but still used the same program, in which participants continued training and testing.

For completeness, we provide below the full details of the experimental stimuli and procedure. We will especially emphasize in full details any differences between our experiment and that of J. Y. Zhang and Yang (2014).

Stimuli, procedure, apparatus, and participants

The basic stimulus was as follows. Within a circular aperture of 8° in diameter that was presented foveally, 400 gray dots on a dark background moved in a single direction with a speed of 10° /s. The duration of the stimulus was 500 ms.

The motion direction discrimination task was a temporal 2AFC. Two motion stimuli, with directions either (22.5°, 22.5° + Δ direction) or (22.5°, 22.5° - Δ direction), were sequentially presented with an interstimulus interval of 200 ms. Participants decided which of the two stimuli moved in a more clockwise direction, with trial-wise feedback. A three-up one-down staircase was used to measure the discrimination threshold. This staircase stopped after 10 reversals, which amounted to approximately 50 trials. The average of the last six reversals was defined as the threshold for the staircase.

The stimuli in the dot number discrimination task were similar, except that participants decided which of the two stimuli had more dots (400 dots, 400 $\pm \Delta$ dot-number), again with trial-wise feedback. The motion

direction of the dots was 202.5°, opposite to the reference direction of 22.5° in motion discrimination, but it was randomly jittered by $\pm 10^{\circ}$ in each trial. The dot number discrimination threshold was measured similarly.

In J. Y. Zhang and Yang (2014), there were two main motion directions. One (22.5°) was for motion discrimination and the other (202.5°) for dot number discrimination. In addition, three other reference directions (112.5°, 247.5°, and 337.5°) were used, along which participants were trained in neither motion nor dot number discrimination. In our experiment, we kept the code unchanged and tested all five reference directions as well.

In J. Y. Zhang and Yang (2014), there were seven sessions. Sessions 1 and 7 were test sessions, in which motion discrimination was tested along each of the five directions. Along each direction, threshold was measured five times, each time with one staircase. The final threshold along this direction was the average of the five measurements. The sequence of the total 25 staircases (5 reference directions \times 5 times) was randomized. Each testing session lasted for about 2 h.

Sessions 2 through 6 were training sessions, in which motion discrimination along 22.5° and dot number discrimination along 202.5° were run in alternating blocks, with a total of 20 blocks (or 20 staircases) per session. Motion discrimination threshold per session was averaged from the 10 staircases, and the dot number discrimination threshold was averaged from the other 10 staircases. Each training session lasted for about 1.5 h.

The luminance of the screen when the entire screen was set at pixel values of [255, 255, 255] was 100 cd/m^2 . This was identical to that in J. Y. Zhang and Yang (2014; Zhang, personal communication). The luminance of the dots was 17.8 cd/m^2 . This luminance was measured by creating a square equal in area occupied by the total number of dots ($400 \times 3 \times 3$ pixels). The luminance of the background was 0 cd/m^2 . These two luminance values were not reported in J. Y. Zhang and Yang (2014) and were not available from the authors after repeated requests. However, because the contrast of the dots was suprathreshold, any difference in contrast of the dots between our study and J. Y. Zhang and Yang (2014) would unlikely be critical. The contrast of the dots is the first difference between the two studies.

The second difference between the two studies is that we used a 17-in. Sony Multiscan G220 computer monitor, whereas a 21-in. Sony G520 monitor was used in J. Y. Zhang and Yang (2014). The screen resolution (1600×1200) and refresh rate (75 Hz) were identical. To match the visual angle as specified in J. Y. Zhang and Yang (2014), our viewing distance was changed from 80 cm to 67 cm. The viewing distance was the third difference.

Six participants, the same number as in J. Y. Zhang and Yang's (2014) experiment 2, were recruited in adherence with the Declaration of Helsinki. They were students from the University of Science and Technology of China, Hefei. The first seven daily sessions were identical to the entire experiment 2 in Zhang and Yang (2014). Namely, in Session 1 and 7, motion discrimination was measured along all the five reference directions. From Session 2 to 6, trainings in motion discrimination and dot number discrimination were conducted in alternating blocks in every daily session.

Starting from Session 8, 10 more training sessions were conducted. In Session 18, motion discrimination was tested again along all the five directions. Afterward, because of a holiday break, only four of the six participants were available for additional training from Session 19 to 22. Motion discrimination along the five directions was tested for the last time in Session 23 for these four participants. Participants ran one session daily, on consecutive days. Because there were only four participants' data after Session 18, these data would be reported by not analyzed.

Results and discussion

The first seven sessions

For ease of comparison, we use here the same measure of learning and transfer in motion discrimination as in J. Y. Zhang and Yang (2014). We first analyzed threshold data in the first seven sessions, which attempted to replicate J. Y. Zhang and Yang (2014). Figure 1 shows the average thresholds as a function of time. Figure 2 shows the average thresholds in the entire experiment, along with every individual participant's data.

We started with a 2×2 analysis of variance (ANOVA) analyzing the motion discrimination thresholds in Session 1 (pretraining) and Session 7 (posttraining), along the motion trained direction and the dot number trained direction. The main effect of time was significant, F(1, 5) = 23.31, p = 0.005, indicating an overall learning effect. Numerically, the mean percentage improvement (MPI), defined as 1 -(postthreshold/prethreshold), was $34.9\% \pm 5.4\%$ for the motion trained direction and $18.7\% \pm 8.4\%$ for the dot number trained direction. In comparison, in J. Y. Zhang and Yang (2014), the corresponding numbers were $28.0\% \pm 4.1\%$ and $26.9\% \pm 3.9\%$, evidence for complete transfer. The main effect of motion direction in our experiment was not significant, F(1, 5) = 1.52, p =0.27. Our data, however, showed a significant Time \times Direction interaction, F(1, 5) = 8.55, p < 0.05. This indicates that the amount of transfer to the dot number



Figure 1. Thresholds in dot number discrimination (green triangle symbols) and motion discrimination (the rest of the five symbols) in the first seven sessions. Session 1 and 7 were preand posttraining sessions, respectively. The blue color represents motion discrimination along the motion trained direction. The red color represents motion discrimination along the opposite direction, along which dot number discrimination was trained. The remaining three open symbols represent the motion discrimination along the three control directions. Sessions 2–6 represent motion direction discrimination training (in color blue) and dot number discrimination (in color green). Error bars represent standard errors of the mean (same as in Figures 2–4).

direction (18.7%) was significantly smaller than the amount of learning along the motion trained direction (34.9%). The transfer index (TI), defined as MPIuntrained/MPI-trained, was 0.48. In all fairness, though, 0.48 was a substantial amount of transfer, although this transfer was incomplete. However, as shown below, this transfer was no greater than the transfer to the control directions.

We also ran a similar ANOVA on motion discrimination thresholds, comparing thresholds between the dot number direction and the control directions. The purpose was to test whether there was any benefit by training the participants with motion stimuli in the dot number discrimination direction, as opposed to no exposure at all. To our surprise, only the main effect of time was significant, F(1, 5) = 8.54, p < 0.05. The main effect of motion direction, F(1, 5) < 1, and the interaction, F(1, 5) = 1.68, p = 0.25, were not significant. As a result, we could not reject the null hypothesis that exposure of motion stimuli provided little benefit to motion discrimination transfer. Numerically, the improvement along the three control directions was 9.7% on average, as compared with 18.7% along the exposed direction.

In J. Y. Zhang and Yang (2014), the improvement along the control directions was approximately 10%. The improvement along the dot number trained direction was 28% (ours was 18.7%) and along the motion trained direction was 26.9% (ours was 34.9%). Therefore, the differences between the two studies were mainly the amount of learning along the motion trained and dot number trained directions. The two differences with opposite signs along these two directions were responsible for the different claims from the two studies.

In J. Y. Zhang and Yang (2014), the amount of learning was compared using a t test between the motion trained and dot number trained directions, and no difference was found. A second t test between the motion trained direction and control directions yielded a significant difference. No direct comparison between the dot number trained and control directions was made. It appears in figure 2a in J. Y. Zhang and Yang (2014) that the latter comparison would have yielded a nonsignificant difference, hence agreeing with our data.

Data analysis of the first 18 sessions

To test whether longer training changed the above pattern of results, we used threshold data from Session 1 and 18 from all six participants to repeat the ANOVA analyses. Here, the total number of training sessions was 15, as compared with 5 in our analysis above and in J. Y. Zhang and Yang (2014).

The new results were completely consistent with the results above, and no beneficial transfer to the dot number direction was significant. Specifically, in the ANOVA comparing between the motion trained and dot number trained directions, the main effect of time was significant, F(1, 5) = 46.45, p = 0.001. The interaction was significant, F(1, 5) = 8.36, p < 0.05. The main effect of direction was not significant, F(1, 5) = 4.41, p = 0.09, indicating a trend that the average threshold along the motion trained direction.

In the ANOVA comparing thresholds between the dot number direction and the three control directions, the main effect of time was significant, F(1, 5) = 16.68, p = 0.009. The interaction was not significant, F(1, 5) < 1, and the main effect of direction was not significant either, F(1, 5) = 1.16, p = 0.33. These results mean that the dot number direction and the control directions were not different in terms of motion direction discrimination.

Numerically, the amount of learning along the motion trained direction over the 18 sessions was 45.9%, as compared with 34.9% in the first seven sessions. The amount of improvement in motion discrimination along the dot number direction over the 18 sessions was 23.9% and that along the three control directions was 21.3% (as compared with 18.7% and 9.7% in the first seven sessions). These numbers mean that five daily training sessions were insufficient for the



Figure 2. Data from the entire experiment. The number of participants was n = 6 for the first 18 sessions, and n = 4 afterwards. Individual data from each of the six participants are also shown. The color scheme is the same as in Figure 1.

session

session



Figure 3. Improvement summary from the entire data in motion discrimination in each of the five directions, and dot number discrimination along the exposure direction in color green. The improvement is defined as (1 – postthreshold/prethreshold) \times 100%. The color scheme is the same as in the other figures.

participants to reach asymptotic performance. Additional training still gave rise to further improvement.

Figure 3 summarizes the amount of learning in motion discrimination along each of the five directions, with the learning defined as $(1 - \text{prethreshold}/\text{postthreshold}) \times 100\%$. Figure 3 also shows the amount of learning in dot number discrimination along the exposed direction, in color green.

We noticed that in the first seven sessions (Figure 3, left), our participants learned not as much in the dot number discrimination task as in J. Y. Zhang and Yang (2014). Our participants' average threshold only dropped from 51 to 47 in dot number. In comparison, the threshold in J. Y. Zhang and Yang (2014) dropped approximately from 65 to 50, a drop that was four times in magnitude as ours. To test whether or not the amount of the second task learning was correlated with the amount of motion discrimination transfer, we correlated the amount of transfer and the amount of second task learning across the six participants. Within the first seven sessions, the correlation coefficient was r= 0.25 (p = 0.64). From Session 8 to 18, r = -0.14 (p = 0.14)0.83). With all data of the 18 sessions considered, r = $0.33 \ (p = 0.53).$

Hence, these correlations were no better than chance. We are aware, however, that these null results do not necessarily imply that the amount of second task learning was irrelevant. Even though the double training literature had emphasized only the role of active (as opposed to passive) exposure of the second task, the amount of second task improvement had never been deemed important, as far as we know. Therefore, it remains an open question whether or not the difference in the amount of learning between our experiment and J. Y. Zhang and Yang (2014) was responsible for the differential transfer. We consider the differences in the amount of learning between the two experiments as due to individual differences.

Experiment 2 in the United States

Methods

The purpose of this experiment was to independently verify at the University of California, Los Angeles (UCLA), the results from Experiment 1. All experimental settings were identical between Experiments 1 and 2, except for the following two differences. The computer monitor at UCLA was a Sony Multiscan E540, as opposed to the Sony G520 in Experiment 1. The viewing distance was changed back to 80 cm to match that in J. Y. Zhang and Yang (2014) and therefore was different from the 67 cm in Experiment 1.

Three participants were recruited who repeated the procedure of experiment 2 of J. Y. Zhang and Yang (2014), except that Participant YGL ran one extra training session by mistake. Afterward, these participants continued to train and test for as long as they were available, giving rise to 28, 30, and 20 sessions, respectively. Participant AST's motion discrimination was also assessed along the five directions at Sessions 18 and 24.

Results and discussion

Data from these three participants are shown in Figure 4. Although no reliable statistics could be obtained from only three participants, the following numbers still provide a clear picture of the participants' learning and transfer.

We start by looking at the first seven sessions, which were identical in procedure to Experiment 1. The MPI along the motion trained direction for participants AST, YGL, and XXS was 7%, 71%, and 36%, respectively, showing large variations between participants. The corresponding MPI in motion discrimination along the dot number direction were -2%, 18%, and 2%. These numbers gave rise to TIs of -0.26, 0.25, and 0.05. These TI numbers were far lower than the 1.2 reported in J. Y. Zhang and Yang (2014). The TI numbers for the dot number direction (-0.26, 0.25, 0.05) were not higher, on average, than for the control directions (0.33, 0.21, 0.45). In other words, exposure of motion along one direction did not result in more transfer to that direction than in unexposed directions.

Next, we look at the overall performance of the three participants through the entire experiment. The MPI along the motion trained direction was 24%, 81%, and 52%, respectively. The corresponding MPI of motion discrimination along the dot number direction was 10%, 42%, and -31%. Numerically, the improvement along the motion trained direction was greater than along the dot number trained direction, for every



Figure 4. Data from three participants at UCLA, one participant per row. The *x*-axis in the left column shows the time, with respect to Day 1, of the sessions. The right column shows the data in the same format as in Figures 1 and 2, for ease of comparison. The symbols are the same as in Figures 1 and 2.

participant. This result does not support complete transfer as found in J. Y. Zhang and Yang (2014).

The TI to the dot number direction for the three participants was 0.41, 0.52, and -0.59, respectively. In comparison, the corresponding TI to the untrained directions was 0.08, 0.35, and 0.10. These numbers indicate large variations among the participants but do not strongly support the hypothesis that motion discrimination transferred more to the dot number directions than to the control directions.

Although all participants in our Experiment 1 ran their experiment in consecutive days, the participants at UCLA had gaps in their sessions for a variety of reasons. One may argue that variations of the training schedule at UCLA may confound our conclusions. We disagree and provide our reasons below.

It should be noted that it is possible to compare with data in J. Y. Zhang and Yang (2014) only in the first seven sessions, because the latter had only seven sessions of data. Our participant XXS in fact ran

through these seven sessions consecutively; therefore, her data were perfectly legitimate to compare. As can be seen in Figure 4 (top row), during posttest at Session 7, the red circle was higher than the blue circle and was nearly level with that at pretest and with the average threshold along the control directions. This means that little transfer of motion discrimination was found to the exposed and unexposed directions.

The same participant XXS could not continue the training during the next 2 months but came back afterward requesting to complete her experiment. She completed the remainder of the training and testing with only small gaps (one or two days). As can be seen in Figure 4, her training thresholds remained comparable to those before the 2-month gap, particularly for the motion discrimination thresholds. Her final testing result showed that although her motion discrimination threshold along the motion trained direction remained low, her motion discrimination threshold along the exposed direction was higher. In fact, it was higher than those along the control directions.

We believe that the scheduling irregularities, rather than confounding our claim, strengthened our claim because the same pattern of results occurred despite the temporal irregularity. Another point to notice is that, irrespective of the scheduling, the testing of motion discrimination along the five directions always took place in the same session. Therefore, the comparison between the five thresholds is always fair.

For participant YGL, the time gaps did not appear to influence the motion discrimination training. Her pretraining motion discrimination threshold shows a large error bar. We do not know the reason, but this is not completely unexpected because this was pretraining performance. She also showed a large error bar in the first posttraining measurement, but this was along one of the control directions. Therefore, it should not be critical in the comparison between the motion trained and exposed directions. YGL also showed large error bars in the dot number discrimination training. She reported that sometimes she was confused and was doing direction discrimination in the dot number discrimination blocks. One can argue that doing direction discrimination in a dot number discrimination block should only facilitate more transfer of motion discrimination to the exposed direction. Still, in both posttests, the red dot was higher than the blue dot. In other words, the motion discrimination threshold along the exposed direction was always higher than along the motion trained direction, suggesting that the transfer was incomplete. Moreover, the threshold along the exposed direction was never lower than along the control directions in these two posttests, suggesting that exposure was ineffective.

For participant AST, large error bars occurred during posttests only. But the error bar along the exposed

direction was either smaller or comparable to other error bars in the same posttest. The threshold along the exposed direction was always higher than along the motion trained direction and was comparable with those along the control directions. As a result, even with the temporal gaps considered, our conclusion remains unchanged.

General discussion and conclusions

In the literature, short- and long-term training were found to give rise to different degrees of specificity. For example, in an orientation discrimination task, Jeter, Dosher, Liu, and Lu (2010) found that long-term training tended to lead to specificity, whereas shortterm learning tended to lead to substantial transfer. According to the reverse hierarchy theory (Ahissar and Hochstein, 1997), long-term training that reaches the very limits of performance involves earlier and hence more specialized cortical areas than short-term learning that may involve higher cortical areas that allow transfer. Hence, long-term learning may be more specific than the short-term learning tested by J. Y. Zhang and Yang (2014).

The aim of the current study was to first replicate the original J. Y. Zhang and Yang (2014) study and then to investigate whether the complete transfer would hold for longer-term training. To our surprise, we could not even replicate the original result in J. Y. Zhang and Yang (2014) with the first seven sessions of data, despite our effort to replicate the experiment as faithfully as possible and in two laboratories. Because we could not find complete transfer in the shorter-term learning, our argument for examining specificity in the longer-term learning was weakened, unfortunately.

The discrepancy of the results between our study and J. Y. Zhang and Yang (2014) raises the question of variability of data (in other words, individual difference) even in short-term learning, in addition to the shortversus long-term training. As far as we could tell, the main difference in methods between our experiments and that in J. Y. Zhang and Yang (2014) was the luminance of the dots, because this information was unavailable from J. Y. Zhang and Yang (2014) after our repeated requests. However, we are doubtful that this difference is responsible for the very different results between the two studies. We wonder if large individual differences, which had been typical in our past studies in motion perceptual learning, were responsible for the different results. Indeed, even in J. Y. Zhang and Yang (2014)'s experiment 1 in which the two tasks were run consecutively rather than in parallel, two of the six participants did not show the transfer effect and were regarded as outliers. In both J. Y. Zhang and Yang (2014)'s experiment 2 and our Experiment 1, each

experiment had only six participants. This small sample size is another possible source of the discrepancies between the two studies. In the literature, Fahle and Henke-Fahle (1996) found that participants varied widely in their pretraining performance, in the amount of learning they could accomplish, and in the speed with which they could accomplish the improvement (see also Astle, Li, Webb, Levi, & McGraw, 2013).

We also noticed that, prior to the J. Y. Zhang and Yang (2014) study in motion discrimination with foveal stimulation, all double training studies were on spatial vision with peripheral stimulation. Some of the studies had been replicated as well (Hung & Seitz, 2014). It remains unclear whether or not spatial and peripheral vision was more robust in transferring learning under the double training regime than motion direction discrimination in foveal vision.

Ultimately, resolving these differences requires additional experiments from independent laboratories.

Keywords: perceptual learning, motion discrimination, double training, staircase, specificity

Acknowledgments

This research was supported in part by a fellowship awarded to Z. L. by the Hanse Institute for Advanced Studies, Delmenhorst, Germany, that allowed collaboration between Z. L. and M. F. This research was supported also in part by the National Natural Science Foundation of China to Z. L. (NSFC 31228009) and to Y. Z. (NSFC 31230032). Correspondence should be sent to either Z. L. or Y. Z. We thank Dr. Junyun Zhang for providing the code in the J. Y. Zhang and Yang (2014) study and Dr. Cong Yu for helpful discussions. We also thank Dr. David Bennett for copyediting in English.

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

References

- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, *387*, 401–406.
- Astle, A. T., Li, R. W., Webb, B. S., Levi, D. M., & McGraw, P. V. (2013). A Weber-like law for perceptual learning. *Scientific Reports*, 3(1158), 1–8.

- 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, 2889– 2894.
- Epstein, W. (1967). Varieties of perceptual learning. New York: McGraw Hill.
- Fahle, M. (2005). Perceptual learning: specificity versus generalization. *Current Opinion in Neurobiology*, 15, 154–160.
- Fahle, M. (1997). Specificity of learning curvature, orientation, and vernier discriminations. *Vision Research*, *37*, 1885–1895.
- Fahle, M., & Henke-Fahle, S. (1996). Interobserver variance in perceptual performance and learning. *Investigative Ophthalmology & Visual Science*, 37, 869–877. [PubMed] [Article]
- Fahle, M., & Poggio, T. (2002). *Perceptual learning*. Cambridge, MA: MIT Press.
- Gibson, E. J. (1969). *Principles of perceptual learning*. New York: Appleton-Century-Crofts.
- Hung, S. C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *Journal of Neuroscience*, *34*, 8423–8431.
- 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.
- Liu, Z. (1995). *Learning a visual skill that generalizes*. Princeton, NJ: NEC Research Institute.
- Liu, Z. (1999). Learning a visual skill that generalizes across motion directions. *Proceedings of the National Academy of Sciences USA*, 96, 14085–14087.
- Rubin, N., Nakayama, K., & Shapley, R. (1997). Abrupt learning and retinal size specificity in illusory-contour perception. *Current Biology*, 7, 461–467.
- Saarinen, J., & Levi, D. M. (1995). Perceptual learning in Vernier acuity: What is learned? *Vision Research*, 35, 519–527.
- Sagi, D. (2011). Perceptual learning in vision research. *Vision Research*, *51*, 1552–1566.

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, 1922–1926.

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.
- Zhang, T., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Decoupling location specificity from perceptual learning of orientation discrimination. *Vision Research*, 50, 368–374.