

Motion perceptual learning: When only task-relevant information is learned

Xuan Huang

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



Hongjing Lu

Psychology Department, University of Hong Kong, Hong Kong



Bosco S. Tjan

Department of Psychology and Neuroscience Graduate Program, University of Southern California, Los Angeles, CA, USA



Yifeng Zhou

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



Zili Liu

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



The classic view that perceptual learning is information selective and goal directed has been challenged by recent findings showing that subthreshold and task-irrelevant information can induce perceptual learning. This study demonstrates a limit on task-irrelevant learning as exposure to suprathreshold task-irrelevant signals failed to induce perceptual learning. In each trial, two random-dot motion stimuli were presented in a two-alternative forced-choice task. Observers either decided which of the two contained a coherent motion signal (detection task), or whether the coherent motion direction was clockwise or counterclockwise relative to a reference direction (discrimination task). Whereas the exact direction of the coherent motion signal was irrelevant to the detection task, detection of the coherent motion signal was necessary for the discrimination task. We found that the detection trainees improved only their detection but not discrimination sensitivity, whereas the discrimination trainees improved both. Therefore, the importance of task relevance was demonstrated in both detection and discrimination learning. Furthermore, both detection and discrimination training along a single pedestal direction transferred to a broad range of pedestal directions. The profile of the discrimination transfer (as a function of pedestal direction) narrowed for the discrimination trainees.

Keywords: motion, perceptual learning, detection, discrimination, random dots, specificity, direction, tuning function

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Introduction

A central question in perceptual learning is—“what is learned?” The answer according to Gibson (1969) is that stimulus information from the environment is extracted with increasing efficiency as a result of experience and practice. Gibson further argued for active learning: “We do not just see, we look; we do not just hear, we listen” (p. 4), implying that perceptual learning is information selective and goal directed. The hypothesis that only task-relevant information is learned has been supported by Ahissar and Hochstein (1993), Shiu and Pashler (1992), and Weiss, Edelman, and Fahle (1993), who found that mere exposure to stimulus information that was task-irrelevant yielded no learning, although this information was suprathreshold. Indeed, it has been shown in the

domain of sensory-motor learning that even if sensory information was task relevant, only active, not passive, self-movement induced sensory-motor learning (Held, 1965; Held & Bossom, 1961; Held & Hein, 1963).

However, recent findings (Amitay, Irwin, & Moore, 2006; Watanabe, Náñez, & Sasaki, 2001) have argued against this hypothesis. Not only was it found that mere exposure to task-irrelevant signals enabled learning, but the signals could also be subthreshold (Watanabe et al., 2001). In a study following on from Watanabe et al. (2001), Seitz and Watanabe (2003) demonstrated that for motion direction identification, learning was only enabled for a task-irrelevant motion direction when it was temporally correlated with task-relevant information. This correlation idea could explain why Shiu and Pashler (1992) and Weiss et al. (1993) did not find learning for task-irrelevant information (Seitz & Watanabe, 2005).

However, it cannot explain why when the task-relevant and -irrelevant stimuli were correlated, there was still no learning of the task-irrelevant stimulus attribute (Ahissar & Hochstein, 1993). Nor can it explain why task-irrelevant learning was enabled without such a correlation in other studies (Amitay et al., 2006; Watanabe et al., 2001). For instance, Watanabe et al. also found that after subthreshold exposure to a pedestal motion direction, suprathreshold direction discrimination was improved. More specifically, in a same–different direction discrimination task, a random-dot motion stimulus was first displayed that moved in the previously exposed pedestal direction, which was followed by a second stimulus that moved either 0° or $\pm 3^\circ$ away. However, the signal for this discrimination, $\pm 3^\circ$ from the pedestal direction, was never exposed. It remains an open question therefore why the never exposed directional difference signal, $\pm 3^\circ$, could be better discriminated as a result of discrimination-irrelevant training (assuming that the bettered discrimination was not solely due to the “same” trials).

These contradictory results in the literature could be at least due to three possibilities: (1) different stimuli because Watanabe et al.’s (2001) stimulus was a letter sequence surrounded by moving random dots, whereas those in earlier studies were static lines; (2) different tasks; and (3) different signal-noise-ratios in the stimuli because Watanabe et al.’s task-irrelevant stimulus was subthreshold, whereas those in earlier studies were suprathreshold.

In the current study, we investigated whether task-irrelevant perceptual learning occurred when task-irrelevant signals were suprathreshold and were also correlated with task-relevant signals. Specifically, we used dynamic dot stimuli to train participants on either a motion detection or a motion discrimination task. The detection task was to identify which of two stimuli had a coherent motion signal defined by a subpopulation of dots all moving in the same direction. The discrimination task was to identify whether the (detected) signal dots moved in a direction clockwise or counterclockwise from a reference direction. Therefore, within these stimuli, the assigned task determined which properties of the stimulus were task relevant. The precise direction of the coherent dots was irrelevant to the detection task. However, detection was necessarily required for the direction discrimination task. Within this paradigm, we found that for detection trainees, subtly varying directional signals yielded no learning for direction discrimination. In comparison, discrimination trainees improved on both discrimination and detection. Consistent with this pattern of results, we also found that the detection trainees’ detection tuning function widened slightly, whereas the discrimination trainees’ discrimination tuning function narrowed.

Studying the effect of training on psychophysically measured tuning functions is important because it provides useful insight into what is actually learned during perceptual learning. This approach parallels physiological

investigations into whether improved orientation discrimination with training is due to steepened neuronal orientation tuning (Ghose, Yang, & Maunsell, 2002; Schoups, Vogels, Qian, & Orban, 2001; Yang & Maunsell, 2004). Changes in behavioral tuning functions as a result of learning or adaptation had also been studied psychophysically (Clifford & Wenderoth, 1999; Prins & Kingdom, 2002; Regan & Beverly, 1985). The study closest to ours was conducted by Koyama, Harner, and Watanabe (2004), who also studied motion detection and discrimination and compared psychophysical tuning functions pre- versus posttraining. Their main finding was that the peak of the detection tuning function remained unchanged, whereas that of the discrimination was shifted (about 7° off). They suggested that the position of the detection peak corresponded to the direction of the signal stimulus and the shifting of the discrimination tuning function improved discrimination by covering the to-be-discriminated directions with the steepened portion of the tuning curve. However, it remains unclear why the peak of the tuning function shifted counterclockwise but not clockwise. In other words, it is unclear why the symmetry was broken. The discrimination tuning function in our current study, in contrast, did not shift after training. Instead it narrowed, presumably to improve discrimination via steepened tuning. As will be seen, there are several methodological differences between Koyama et al. and our current study that may account for the different results.

Method

Stimuli and task

Figure 1 illustrates the motion stimuli in a trial. Viewing the stimuli, a participant performed either a motion detection or a discrimination task. Specifically, one stimulus in a trial was noise with dots moving in random directions at a constant speed. The other stimulus contained a certain proportion of signal dots that were embedded in noise and moved in a single direction. In the detection task, a participant judged which of the two stimuli was signal. In the discrimination task, the participant judged the signal direction to be either clockwise or counterclockwise to the longer arm of the fixation cross. This orientation was defined as the pedestal direction that bisected the two possible signal directions.

In a trial, each motion stimulus was presented for 200 ms and consisted of 200 black dots (0 cd/m^2) in a gray (13 cd/m^2) circular aperture (10°) with a red fixation disk (14 cd/m^2 , 0.4°) at the center. The size of each dot was 0.1° , and the speed was 3.75 deg/s . The red fixation disk was shown for 500 ms between the two motion stimuli. After the second motion stimulus, a red fixation

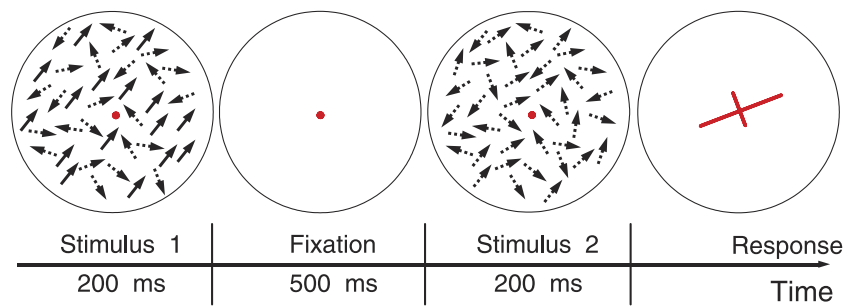


Figure 1. Schematic illustration of one trial. One of the two stimuli (the first, in this illustration) consisted of a certain proportion of signal dots (illustrated as solid arrows) all moving in one direction and embedded in noise dots (dashed arrows). The other stimulus consisted of noise dots. After the motion stimuli, a red fixation cross with a longer arm oriented along the bisecting pedestal direction was shown until a response was made. For detection, the task was to identify which stimulus was the signal. For discrimination, the task was to identify whether the signal stimulus moved clockwise or counterclockwise relative to the longer arm of the fixation cross.

cross was shown, with one long arm and one short arm (2.0° and 0.6° , respectively). This fixation cross remained in view until the onset of the next trial, which started one second after a response was made. In the detection task, participants were shown the pedestal direction at the beginning of a block via a blue dot positioned along the long arm of the fixation cross. In the discrimination task, participants were shown the two signal motion directions via two blue dots.

Procedure

The entire experiment consisted of six steps. We first summarize the main points of these steps, followed by more detailed descriptions.

1. Practice was given to reduce any task familiarization effect.
2. Psychometric functions were measured to determine the stimulus parameters to be used in Steps 3 and 4. These parameters were tailor-made for each participant.
3. Behavioral tuning functions for detection and discrimination were measured across a range of pedestal motion directions.
4. Participants were trained at either the detection or discrimination task.
5. Step 2 was repeated.
6. Step 3 was repeated.

Practice

Participants were randomly assigned to one of two pedestal directions: 45° or 135° . For the detection practice, the signal coherence was set to 50% and the directional signal differed from the pedestal direction by 8° . For the discrimination practice, the signal coherence was 50% and the directional difference was 40° . Participants practiced for at least 60 trials in each task until they reached 95% correct. Feedback was provided per trial.

Psychometric functions

Psychometric functions were measured along the pedestal direction not used in practice (e.g., 45° if 135° was used in practice). First the detection psychometric function was measured at six levels of signal coherence: 5%, 10%, 15%, 20%, 30%, and 40%. The directional signal was kept at 8° . The psychometric function was measured in a blocked and a counterbalanced design, with 50 trials per block. The discrimination psychometric function was then measured at six directional differences: 3° , 5° , 8° , 11° , 15° , and 30° . The signal proportion was chosen so that it gave rise to 95% correct detection. The same blocked and counterbalanced design was used. It took approximately 40 min to measure each psychometric function. No feedback was provided. Both detection and discrimination psychometric functions were measured twice pretraining and once posttraining. The first pretraining measurement was considered practice and was not analyzed.

Directional tuning functions

From the two psychometric functions measured for each individual participant, we chose the signal coherence level that gave rise to 80% correct for detection and the directional difference that gave rise to 80% correct for discrimination. Using this fixed stimulus, we measured detection and discrimination in seven pedestal directions: 0° , $\pm 30^\circ$, $\pm 60^\circ$, and $\pm 90^\circ$, where 0° was the direction previously used for the psychometric function measurements. Each behavioral tuning function was measured using a blocked and counterbalanced design, with a total of 560 trials without feedback. It took approximately 30 min to measure each tuning function.

Training

Participants were randomly assigned as either detection or discrimination trainees. For the detection trainees,

QUEST (Watson & Pelli, 1983) was used to vary the signal proportion (starting at 40% for all participants) to keep the participant's performance at 80% correct detection. The directional difference was kept constant at the 80% correct threshold for discrimination measured in Step 2. For the discrimination trainees, QUEST was used to vary the directional difference (starting at 20° for all participants) to keep the performance at 80% correct discrimination. The signal proportion was kept constant at the 80% correct threshold for detection measured in Step 2. Each participant was trained for either 8 or 15 days. Each daily session had 864 trials that lasted for about 60 min. Feedback was provided per trial.

Apparatus

The experiment used MatLab (MathWorks, Inc.) with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and was run on a P4 1.7G PC computer in a dimly lit room. The display was a 17-in. Sony G220 with a resolution of 1,024 × 768 pixels and a vertical refresh rate of 75 Hz. All the participants viewed the stimuli binocularly, with a chin rest to stabilize the viewing distance at 57 cm.

Participants

Nineteen observers from the University of Science and Technology of China participated. Ten trained with the detection task and nine trained with the discrimination task. Four additional observers participated in the pilot study (two in each training group). The only difference for these pilot participants was that the pretraining behavioral tuning functions were not measured. Data from these four participants were included for analysis when applicable.

All participants were 20–25 years of age with normal or corrected-to-normal vision and were naive as to the purpose of the study.

Results

Unless specified otherwise, ANOVA and its planned comparisons were used in data analysis. All error bars in the data plots represent standard errors.

Learning

Both the detection and discrimination trainees improved their performance as indicated by their reduced thresholds. Figure 2 shows each participant's thresholds in the first and last training days, respectively. This learning was statistically significant: detection, $F(1, 11) = 91.58$, $p < .001$; discrimination, $F(1, 10) = 34.46$, $p < .001$.

Task-relevant learning

Figure 3 shows pre- and posttraining psychometric functions for the detection and discrimination trainees. For the detection trainees, there was a significant overall improvement in detection (Figure 3A), $F(1, 21) = 26.57$, $p < .001$, whereas the overall discrimination performance changed little after detection training (Figure 3C), $F(1, 21) < 1$. For the discrimination trainees, both detection and discrimination psychometric functions improved (Figures 3B and 3D): detection, $F(1, 21) = 28.87$, $p < .001$; and discrimination, $F(1, 21) = 58.71$, $p < .001$. This pattern of results was further supported by a significant three-way interaction between measurement (pre- vs.

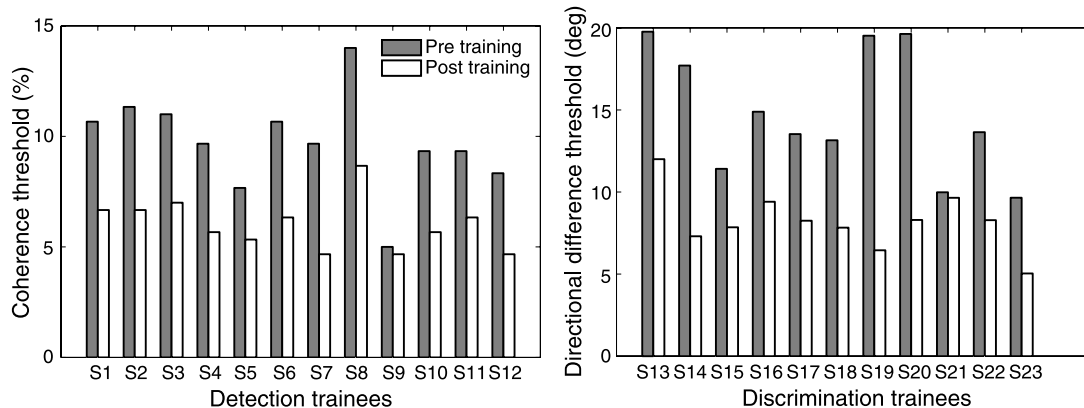


Figure 2. Thresholds at the first (dark bars) and last (light bars) training days for each trainee. Left: detection training with a constant directional difference and constant detection performance at 80% correct. Right: discrimination training with a constant signal proportion and constant discrimination performance at 80% correct.

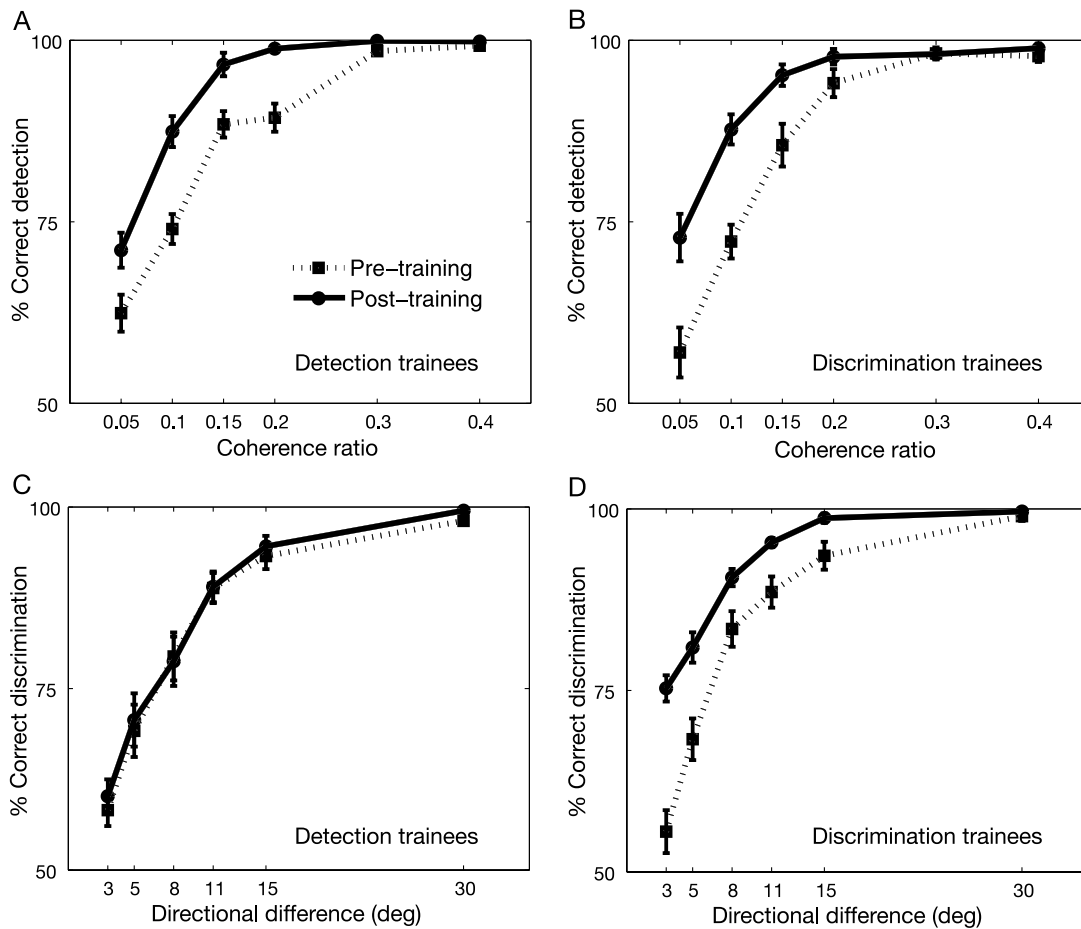


Figure 3. Pretraining (dotted) and posttraining (solid) psychometric functions for detection (top) and discrimination (bottom). Left column: the detection trainees; right column: the discrimination trainees.

posttraining), task (detection vs. discrimination), and training (detection vs. discrimination), $F(1, 21) = 14.68$, $p = .001$. This interaction indicates that learning transferred from discrimination to detection, but not vice versa. This asymmetry of transfer suggests that only task-relevant stimulus information was learned.

The asymmetric transfer cannot be attributed to differential learning magnitudes on the two training tasks. We compared the post/pre percent correct ratio of the detection trainees on the detection task and that of the discrimination trainees on the discrimination task. No significant difference was found, $F(1, 21) = 2.24$, $p = .15$ (mean ratios: 1.09 for the detection trainees and 1.14 for the discrimination trainees).

Transfer of detection and discrimination to untrained pedestal directions

We examined how learning transferred from the trained to untrained pedestal directions and how learning affected the shape of the behavioral tuning functions. We first focused on how perceptual learning affected the behavioral tuning functions measured with the same task,

namely, the change of detection tuning functions for the detection trainees and the change of discrimination tuning functions for the discrimination trainees.

ANOVA revealed a significant main effect of overall improvement across all pedestal directions for both detection, $F(1, 9) = 21.38$, $p = .001$, and discrimination, $F(1, 8) = 23.02$, $p = .001$. The interactions between training and pedestal directions were not significant: detection, $F(6, 54) < 1$; discrimination, $F(6, 48) = 1.15$, $p = .35$. This indicates that motion detection and discrimination training along one pedestal direction transferred more widely to other pedestal directions than has been found in previous studies (Ball & Sekuler, 1982, 1987). This difference was likely due to different training technique; that is, the method of constant accuracy was used in the current study, whereas the method of constant stimuli was used in the previous studies. This broad transfer was unlikely due to task familiarization because all participants had been well practiced.

We used the von Mises (1918) function to fit the behavioral tunings. This function is unimodal and symmetric: $y(\theta) = a + b \exp[\kappa \cos(\theta - \mu)]$, where μ is the peak direction and $1/\kappa$ is the bandwidth. The peaked pretraining functions were most likely due to learning

along the to-be-trained pedestal direction during the psychometric measurements (2,400 trials in total). In fact, the amount of this learning was comparable or even larger than that due to training. It is likely that the variety of the stimuli and the blocked design used in the psychometric measurements was effective for this learning. Figure 4 shows the pre- and posttraining detection tuning functions for the detection trainees (10 participants) and the discrimination tuning functions for the discrimination trainees (9 participants).

Widening and narrowing of behavioral tuning functions

Results from the transfer analyses were mixed about the putative widening or narrowing of tuning functions from pre- to posttraining. On the one hand, the nonsignificant interactions between training and pedestal directions indicated that the tuning functions changed shape nonsignificantly from pre- to posttraining. On the other hand, the von Mises (1918) fits indicated numerically that the detection tuning function was slightly widened posttraining whereas the discrimination tuning function narrowed (Figure 4).

Upon closer examination of each individual participant's tuning, it appeared that this inconsistency may have been due to noise in the measurement. Although the von Mises (1918) fitting to the group average performance was good ($R^2 \geq .90$), the fitting to each individual participant's performance often yielded relatively poor goodness-of-fit. That is to say, an individual participant's tuning function was often neither unimodal nor symmetric, and the peak of the function was often not at the trained pedestal direction. These large individual differences are not uncommon in perceptual learning, so caution was in order

when interpreting the ANOVA interaction effects and the von Mises fittings.

Accordingly, the following ANOVA planned comparisons were conducted. The performance at the middle three pedestal directions and the performance at the four outer directions were compared using the following contrast $[1/4 \ 1/4 \ -1/3 \ -1/3 \ -1/3 \ 1/4 \ 1/4]$. Given that the underlying assumption of this comparison was to use a linear contrast to characterize the width of a nonlinear tuning function, we verified this assumption by correlating this contrast with κ in the von Mises (1918) function. Across a large range of κ values, the correlation coefficient was high, $r = .97$. Having justified this planned comparison, we found a significant width change of the discrimination tuning for the discrimination trainees, posttraining as compared with pretraining, $F(1, 8) = 10.83$, $p = .01$, but not of the detection tuning for the detection trainees, $F(1, 9) < 1$.

Next, we performed the following nonparametric analysis with minimal assumptions. This analysis was necessary because, by not assuming any specific form of the tuning function and therefore by taking the raw data as they were, we could perform a more direct test. We observed that if a function widens, the resultant difference function necessarily has a trough at the center. Conversely, if a function narrows, it must have a peak at the center. Therefore, the following two criteria were used to determine whether each participant's tuning function widened or narrowed.

1. If a difference function had peaks and troughs, the peak or the trough closest to the trained pedestal direction (the center) was chosen.
2. If a peak and a trough were equally close to the center, the one with a larger difference from the mean was chosen.

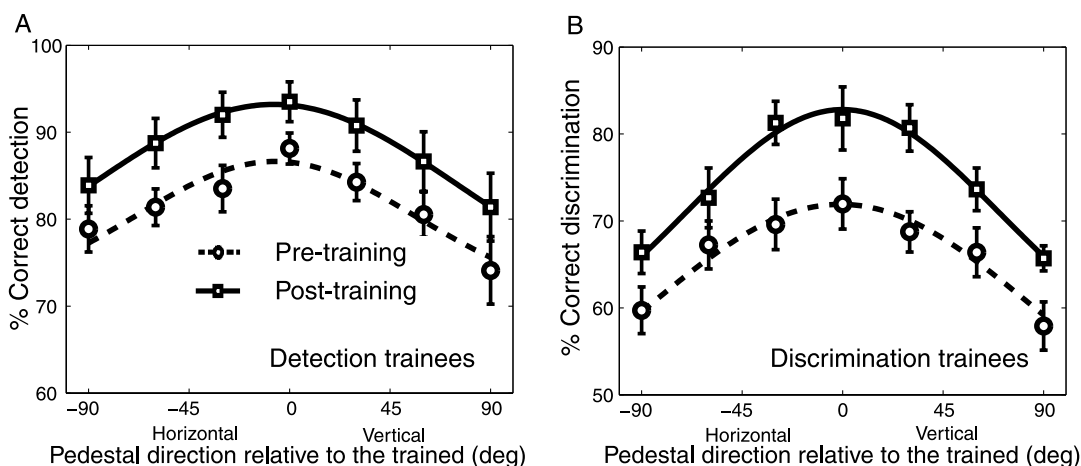


Figure 4. Pretraining (dashed) and posttraining (solid) behavioral tuning functions showing detection for the detection trainees (A) and discrimination for the discrimination trainees (B). 0° in the abscissa is defined as the trained pedestal direction for each trainee. 45° always corresponds to the upward direction, and -45° corresponds to horizontal directions.

With only these two criteria, we found that 9 out of the 10 detection trainees gave rise to a trough, indicating widening of the detection tuning function ($p = .02$, exact binomial sign test). Of the nine discrimination trainees, eight gave rise to a peak, indicating narrowing of the discrimination tuning function ($p = .04$).

To further check the specificity of the above results, we examined the discrimination difference function of the detection trainees. Five out of the 10 participants gave rise to peaks. For the detection difference function, four out of the nine discrimination trainees gave rise to a peak. These results were not statistically significant, indicating that the results of widening and narrowing were specific to the training and test.

Finally, for completion, we show in Figure 5 the discrimination tuning functions of the detection trainees and the detection tuning functions of the discrimination trainees, fitted with von Mises (1918) functions. ANOVA revealed a significant main effect of discrimination training on the overall improvement of performance across different pedestal directions for detection, $F(1, 8) = 6.95$, $p = .03$. No other results were statistically significant. Importantly, results shown in this figure were consistent with the conjecture that correct detection is necessary for discrimination. Consequently, for a stimulus giving rise to 80% correct detection, discrimination of the same stimulus could be at best 80% correct. Likewise, for a stimulus giving rise to 80% correct discrimination, detection of the same stimulus had to be at least 80% correct. Hence, it makes sense that, pretraining, discrimination was approximately 65% correct with the detection stimuli (recall that the angular size for discrimination was chosen to give rise to 80% correct performance, so $80\% \times 80\% = 64\%$), and detection was greater than 80% correct with the discrimination stimuli.

In summary, the results indicate that the detection tuning was slightly widened for the detection trainees and that the discrimination tuning was narrowed for the

discrimination trainees. In other words, detection training transferred broadly from the trained to untrained pedestal directions, whereas discrimination training was relatively more specific to the trained pedestal direction.

Discussion

The current study yielded three main results. The first was that learning of motion discrimination transferred to motion detection, but not vice versa. This indicated that the precise motion directional signal, which was not relevant to detection but nevertheless present throughout, was not learned during motion detection training. It should be noted that the directional signal, yielding 80% discrimination accuracy at pretraining, was well above threshold. In comparison, the motion signal used in training by Watanabe et al. (2001) was subthreshold. In this sense, the two studies are not directly comparable. Nevertheless, although it is surprising that observers in Watanabe et al. could use subthreshold motion signals to improve at both motion detection and discrimination during letter identification training, it also seems surprising that observers in the current study could not use suprathreshold signals for motion direction discrimination during motion detection training.

In comparison to this nontransfer from detection to discrimination, the transfer from discrimination to detection was expected. In our task, to correctly figure out in which direction the signal dots were moving, it was first necessary to identify which of the two stimuli contained the signal. Hence, detection was a task-relevant prerequisite for discrimination. This being said, it is still surprising that although the motion coherence was strong enough to give rise to 80% accuracy in detection at pretraining, the participants still managed to further

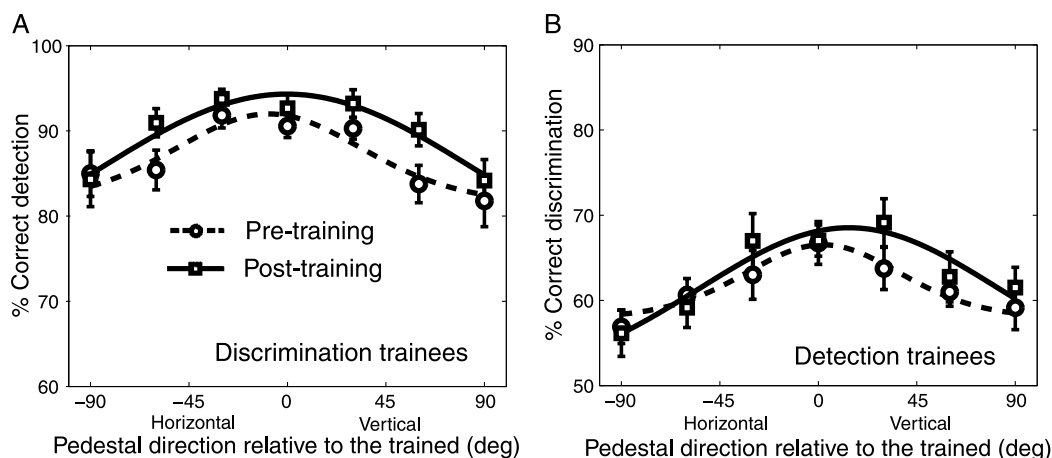


Figure 5. Pretraining (dashed) and posttraining (solid) behavioral tuning functions for detection by the discrimination trainees (A) and for discrimination by the detection trainees (B).

improve their detection abilities. In other words, given that the motion coherence was already at 80% correct for detection, this task transfer was more surprising than if the motion coherence had been lower and therefore required participants to try harder to detect the signal. It is possible that we found only task-relevant perceptual learning because we used suprathreshold task-irrelevant signals, whereas subthreshold task-irrelevant signals were used by Watanabe et al. (2001) and Seitz and Watanabe (2003). It has been postulated that only subthreshold, task-irrelevant signals could be learned because suprathreshold, task-irrelevant signals would be actively inhibited by the brain (Tsushima, Sasaki, & Watanabe, 2006).

The second result from the current study was that as a result of training, detection and discrimination, as measured by their behavioral tuning functions, substantially improved across a broad range of pedestal motion directions ($\pm 90^\circ$ from the trained) as shown in Figure 4. This result is consistent with previous findings that when the task was easier (80% correct), learning transferred more readily to untrained pedestal directions (Ahissar & Hochstein, 1997; Liu, 1999; Liu & Weinshall, 2000; Thompson & Liu, 2006). We conjecture that another reason for this directionally broad range of transfer was due to the training method, in which stimuli were gradually degraded to maintain 80% accuracy as the trainees improved. This issue is currently under investigation.

The third result was that the directional tuning function for detection was slightly widened as a result of detection training, whereas that for discrimination was narrowed as a result of discrimination training. This finding is consistent with the hypothesis that only task-relevant information was learned. Specifically, in motion detection training, both of the two possible motion directions had to be monitored whereas the difference between them from the reference pedestal direction could be ignored because this difference carried no relevant information for completing the detection task. Given that these two directions flanked the pedestal direction and that their directional difference was moderate, it is reasonable for the tuning function to widen in order to improve performance. We note that this was a reasonable but not necessary solution for detection learning. For instance, the entire tuning function could have simply shifted upward without changing its bandwidth. The latter change would have accomplished similar improvement although less efficiently because no signal dots would have moved exactly along the peak direction.

Relative to detection training, discrimination training had a different purpose. In this case, distinguishing between (rather than combining) the two possible motion directions was critical. It was important therefore for the visual system to figure out whether the signal dots moved clockwise or counterclockwise relative to the reference pedestal direction. In this regard, although steepened neural tuning functions were plausible, it remains unclear

how this could enhance discrimination while keeping the tuning function symmetric. We choose not to speculate further on underlying neuronal mechanisms as the most important results from this study were at the behavioral level and we lack sufficient evidence to determine specific neural mechanisms.

These results were also consistent with the previous findings that easier tasks generated transfer to a broader range of motion directions (Liu, 1999; Liu & Weinshall, 2000). Recall that the stimuli used to measure the tuning functions had a signal proportion that yielded 80% correct in detection at pretraining and a directional difference that yielded 80% correct in discrimination when detection was 95% correct. This means that the stimuli were easier to detect than to discriminate. In this sense, the results were consistent with the notion that the easier task (detection) transferred more broadly in pedestal direction than the harder task (discrimination).

We acknowledge that the results regarding the widening and narrowing of tuning functions need to be taken with caution because not all analyses converged on the same conclusions. We made our conclusions primarily based on the nonparametric analysis because minimal assumptions were made. We also noticed the difficulty of finding a widening tuning function as a result of training. This is because a behavioral tuning function is necessarily flat at pretraining (ignoring the difference between cardinal and oblique directions). Therefore, any initial training will either keep the function flat or narrow its bandwidth, but never widen the function. Consequently, to find widening, a function necessarily has to be narrowed first and then widened. It is therefore difficult to compare two stages of training and find widening, particularly because it is common to find large individual differences in perceptual learning.

Finally, we compare the current study with that of Koyama et al. (2004). In Koyama et al., the peak of the behavioral tuning function for motion detection was unchanged, whereas that for motion discrimination was shifted counterclockwise. These tuning functions were measured at a finer scale (5° – 10° per step as opposed to 30° in the current study), although the bandwidths of the tuning functions were not examined. It is unclear, however, why the peak of the discrimination tuning function shifted counterclockwise but not clockwise. There were also differences in detail. In Koyama et al., the stimuli used for detection and discrimination training were identical, and hence the training was based on the method of constant stimuli. In the current study, the stimuli used for detection and discrimination training were similar but not identical because the stimuli were tailor-made for each participant and task. Furthermore, the training employed the method of constant performance. For detection training, Koyama et al. used a two-alternative forced-choice task, similar to that employed in the current study. In each trial, two stimuli were presented: one was noise, the other was signal embedded

in noise. For discrimination, Koyama et al. rearranged the entire set of detection stimuli so that the two stimuli in a trial could be both signal, one signal and one noise, or both noise. The participants decided whether the directions of the two stimuli were the same or different. Although trials with noise stimuli were excluded from analysis because all trials were randomly interleaved and because it is difficult for the visual system to hold multiple decision criteria (Gorea & Sagi, 2000), it is unclear what decision criterion or criteria the participants used in the discrimination task. Because of these methodological differences, the current study does not directly contradict the results of Koyama et al. Rather, the differences in methodology are too numerous for a meaningful comparison.

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Corresponding author: Yifeng Zhou.

E-mail: zhouy@ustc.edu.cn.

Address: School of Life Sciences, University of Science and Technology of China, Hefei, Anhui 230027, China.

References

- Ahissar, M., & Hochstein, S. (1993). Attentional control of early perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, *90*, 5718–5722. [PubMed] [Article]
- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, *387*, 401–406. [PubMed]
- Amitay, S., Irwin, A., & Moore, D. R. (2006). Discrimination learning induced by training with identical stimuli. *Nature Neuroscience*, *9*, 1446–1448. [PubMed]
- Ball, K., & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science*, *218*, 697–698. [PubMed]
- Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, *27*, 953–965. [PubMed]
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436. [PubMed]
- Clifford, C. W., & Wenderoth, P. (1999). Adaptation to temporal modulation can enhance differential speed sensitivity. *Vision Research*, *39*, 4324–4331. [PubMed]
- Ghose, G. M., Yang, T., & Maunsell, J. H. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neurophysiology*, *87*, 1867–1888. [PubMed] [Article]
- Gibson, E. J. (1969). *Principles of perceptual learning and development* (p. viii, 537 pp.). New York: Appleton-Century-Crofts.
- Gorea, A., & Sagi, D. (2000). Failure to handle more than one internal representation in visual detection tasks. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 12380–12384. [PubMed] [Article]
- Held, R. (1965). Plasticity in sensory-motor systems. *Scientific American*, *213*, 84–94. [PubMed]
- Held, R., & Bossom, J. (1961). Neonatal deprivation and adult rearrangement: Complementary techniques for analyzing plastic sensory-motor coordinations. *Journal of Comparative and Physiological Psychology*, *54*, 33–37. [PubMed]
- Held, R., & Hein, A. (1963). Movement-produced stimulation in the development of visually guided behavior. *Journal of Comparative and Physiological Psychology*, *56*, 872–876. [PubMed]
- Koyama, S., Harner, A., & Watanabe, T. (2004). Task-dependent changes of the psychophysical motion-tuning functions in the course of perceptual learning. *Perception*, *33*, 1139–1147. [PubMed]
- Liu, Z. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 14085–14087. [PubMed] [Article]
- Liu, Z., & Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research*, *40*, 97–109. [PubMed]
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442. [PubMed]
- Prins, N., & Kingdom, F. A. (2002). Orientation- and frequency-modulated textures at low depths of modulation are processed by off-orientation and off-frequency texture mechanisms. *Vision Research*, *42*, 705–713. [PubMed]
- Regan, D., & Beverly, K. I. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America A, Optics and image science*, *2*, 147–155. [PubMed]
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, *412*, 549–553. [PubMed]

- Seitz, A., & Watanabe, T. (2005). A unified model for perceptual learning. *Trends in Cognitive Sciences*, 9, 329–334. [[PubMed](#)]
- Seitz, A. R., & Watanabe, T. (2003). Psychophysics: Is subliminal learning really passive? *Nature*, 422, 36. [[PubMed](#)]
- Shiu, L. P., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception & Psychophysics*, 52, 582–588. [[PubMed](#)]
- Thompson, B., & Liu, Z. (2006). Learning motion discrimination with suppressed and unsuppressed MT. *Vision Research*, 46, 2110–2121. [[PubMed](#)]
- Tsushima, Y., Sasaki, Y., & Watanabe, T. (2006). Greater disruption due to failure of inhibitory control on an ambiguous distractor. *Science*, 314, 1786–1788. [[PubMed](#)]
- von Mises, R. (1918). Über die “Ganzzahligkeit” der Atomgewichte und verwandte Fragen. *Physikalische Zeitschrift*, 19, 490–500.
- Watanabe, T., Náñez, J. E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature*, 413, 844–848. [[PubMed](#)]
- Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, 33, 113–120. [[PubMed](#)]
- Weiss, Y., Edelman, S., & Fahle, M. (1993). Models of perceptual learning in Vernier hyperacuity. *Neural Computation*, 5, 695–718.
- Yang, T., & Maunsell, J. H. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience*, 24, 1617–1626. [[PubMed](#)] [[Article](#)]