

perceptual learning experiments are performed with a specific stimulus condition (e.g., a specific orientation or retinal location), and learning is often specific to this condition. The specificity has prompted many perceptual learning researchers to propose that the observed sensitivity improvements may result from tuning changes in early visual neurons (Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Teich & Qian, 2003) or reweighting of the responses of these neurons that respond to the specific stimulus condition (Mollon & Danilova, 1996; Doshier & Lu, 1998, 1999; Yu, Klein, & Levi, 2004; Doshier, Jeter, Liu, & Lu, 2013). More recent evidence indicates that even specific perceptual learning can be rendered significantly and often completely transferrable to new stimulus conditions with double training (Xiao et al., 2008; Zhang et al., 2010; Zhang, Cong, Klein, Levi, & Yu, 2014; Wang et al., 2016; Xiong, Zhang, & Yu, 2016), prevention of stimulus adaption (Harris, Gliksberg, & Sagi, 2012), or covert attention to the trained stimuli (Donovan, Szpiro, & Carrasco, 2015). It is thus unlikely that learning is limited to sensory neurons directly activated by the training stimuli or reweighting of the responses of these neurons. Rather, more general rules for response reweighting may have been abstracted through reweighting responses to a specific stimulus, so that perceptual learning is transferrable in principle (Xiao et al., 2008; Zhang et al., 2010; Wang et al., 2016).

Here we present evidence for a new format of perceptual learning that by design may bypass the above early plasticity or response reweighting mechanisms of learning. Our observers practiced orientation discrimination of a Gabor stimulus at 12 locations and 4 orientations. The stimulus location and orientation were changed from trial to trial, but one location/orientation combination served as the pre-/post-training condition and was skipped; therefore, there were 47 training conditions and

Training improves the sensitivity of humans to fine differences of basic visual features. Typically, these

1 pre-/post-training test condition. During training, each condition was repeated twice per block of trials, for a total of 12 trials per daily session. The repeats of the same condition were separated by 4 to 5 minutes, on average, within a session. The purpose of having very sparse trials with very long time gaps for each training condition was to prevent learning if each training condition was practiced alone. Therefore, significant perceptual learning with multiple stimulus conditions would suggest that the learning is less likely based on early neural plasticity or response reweighting associated with each particular condition. Rather, it more likely occurs on the basis of abstracted evidence from multiple stimulus conditions that are not specific to particular stimulus orientations and locations.



Sixty-eight observers (17–28 years old; 32 males and 36 females) with normal or corrected-to-normal vision were recruited from undergraduate and graduate students. They were new to psychophysical experiments and were naïve to the purposes of the study. The experiments were approved by the Peking University institutional review board. Informed written consent was obtained before data collection from each observer. This work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

The stimuli were generated with Psychtoolbox-3 (Pelli, 1997) and presented on a 21-in. CRT monitor (1024 × 768 pixels; pixel size, 0.39 × 0.39 mm; 120-Hz frame rate; 46.0 cd/m² mean luminance). The screen luminance was linearized by an 8-bit look-up table. Viewing was binocular at a distance of 1 m, and a chin and head rest stabilized the head. Viewing was through a circular opening (diameter = 17°) in black cardboard that covered the rest of the monitor screen. Experiments were run in a dimly lit room. An EyeLink-1000 eye tracker (SR Research, Kanata, Ontario, Canada) monitored eye movements. A trial where the eye position deviated from the fixation point for >2° would be immediately aborted and later repeated. The mean deviation from the fixation across all trials in all observers was 0.71°, and the mean of individual standard deviations was 0.36°; therefore, our data were not significantly affected by improper eye movements.

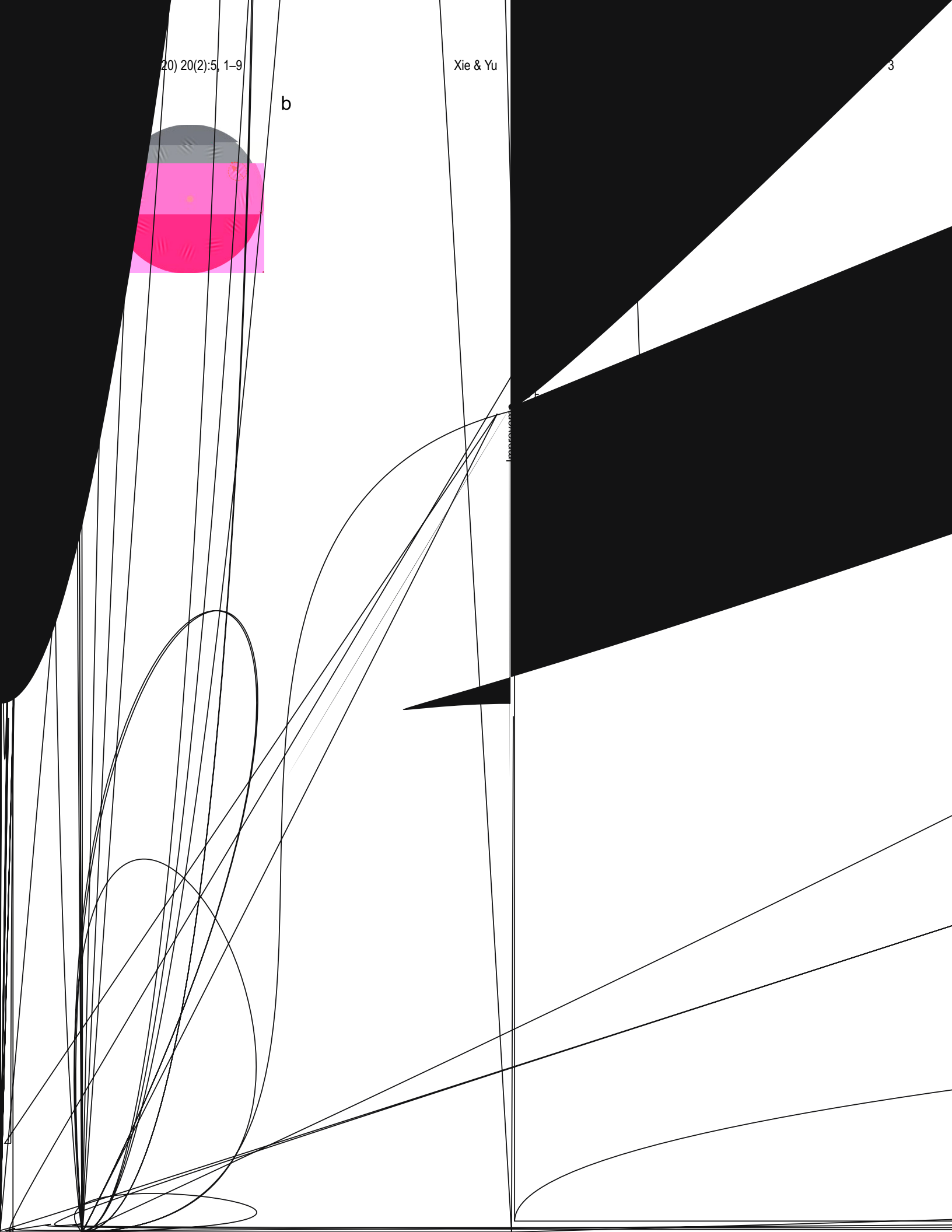
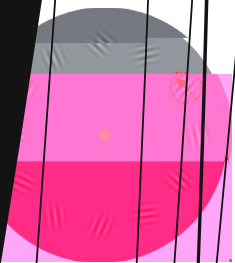
The stimuli included Gabor gratings (Gaussian-windowed sinusoidal grating) and symmetric dot

patterns. The Gabor stimulus was 3 cpd in spatial frequency, 47% in contrast, 0.68° in standard deviation, and random in phase for every presentation. A symmetric dot pattern consisted of 18 pairs of bilaterally symmetric white dots (0.1° diameter), which were confined to an area divided into 18 × 18 invisible square compartments (0.16° × 0.16° each). The placement of the 18 dots on one side of the symmetry axis (within 18 rows by 9 columns of available compartments) was subject to the following constraints: (1) no dot was placed in the column of compartments nearest to the symmetry axis; (2) for the other 8 columns, 2 of them were randomly chosen to hold 3 dots in each column, and each of the remaining 6 columns contained 2 dots; (3) only one dot was allowed in each of the 18 rows by randomly assigning row numbers to the 18 dots on one side of the symmetric pattern; and (4) the location of each dot was randomly jittered by 0° to 0.04° from the compartment center. After positioning the 18 dots on one side of the symmetry axis, the whole symmetric pattern was generated by placing 18 mirror-imaged dots on the other side. The dot pattern was regenerated for each stimulus presentation. A Gabor or symmetric dot pattern was presented on a mean luminance screen background at 5° retinal eccentricity.

The orientation discrimination threshold was measured with a two-interval, forced-choice staircase procedure. In each trial, a small fixation cross preceded the first interval by 500 ms and stayed throughout the trial. The stimuli at the reference orientation and the test orientation (reference + Δori) were shown in two 100-ms (for a Gabor) or 200-ms (for a dot pattern) stimulus intervals, respectively, in a random order. The two stimulus intervals were separated by a 500-ms interstimulus interval. The observers judged which stimulus interval contained the more clockwise-oriented stimulus. In addition, the contrast discrimination threshold (for Gabor only) was measured with a similar procedure, except that the stimulus contrast was varied (reference + Δcontrast). The observers judged which interval had higher contrast. Auditory feedback was given on incorrect responses in both orientation and contrast discrimination tasks.

Thresholds were estimated following a three-down/one-up staircase rule that converged at a 79.4% correct response rate. The step size of the staircase was 0.05 log units. For pre-/post-training testing, each staircase consisted of four preliminary reversals and six experimental reversals (approximately 50–60 trials). The geometric mean of the experimental reversals was taken as the threshold for each staircase run. During training with multiple random or rotating conditions (see Training designs, below), a single staircase varied the orientation or contrast difference for all stimulus conditions through 94 trials (two for each condition). The number of training trials with the baseline group

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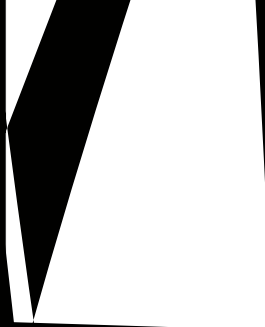
sizes (Xiong et al., 2016; Xiong, Tan, Zhang, & Yu, 2019). We basically followed this rule of thumb to determine the sample size (8 to 10 in all experiments).

Data were analyzed with SPSS Statistics 20.0 (IBM, Armonk, NY). The learning effects were measured by the percent threshold improvements from pre- to post-test session or from first to fifth training session. One-way analysis of variance (ANOVA) and *t*-tests were used to analyze the threshold improvements. The statistical powers were measured with Cohen's *d* in *t*-tests and partial eta-squared in ANOVA.

We were interested in two learning effects: first and in particular, whether training with multiple stimulus conditions would generate significant learning; and second, whether such learning could transfer to the untrained pre-/post-training condition, and how much the transfer would be when compared to the baseline group that practiced the pre-/post-training condition directly.

The first learning effect for the multiple stimulus conditions was calculated as the percent threshold improvement from the first to the fifth (last) training session (Figures 1b and 1c). For the random group ($n = 10$), the stimulus location and orientation were randomized from trial to trial. The orientation thresholds with multiple stimulus conditions were about three times as high as the pre-/post-training condition that contained a single stimulus, and training reduced the thresholds with multiple stimulus conditions by $37.0 \pm 6.2\%$ ($t_9 = 5.93$; $p < 0.001$; 95% confidence interval [CI], 22.9–51.1; Cohen's $d = 1.87$; two-tailed paired *t*-test here and in later analyses unless otherwise specified) (Figures 1b and 1g). We suspected that the higher thresholds might have resulted from increased stimulus uncertainty due to stimulus randomization. Therefore, we had the rotating group ($n = 8$) practice the same stimuli while the stimulus location and orientation were rotated. Such orderly stimulus presentations would reduce stimulus uncertainty and facilitate learning (Kuai, Zhang, Klein, Levi, & Yu, 2005; Zhang et al., 2008). However, the orientation thresholds with rotating conditions were also more than twice as high as those with the pre-/post-training condition, indicating that the high thresholds were not much related to stimulus uncertainty. Training reduced orientation thresholds

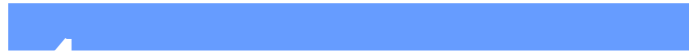
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current effort is to establish a preferred retinal locus (PRL) as the new “fovea” for peripheral viewing (Kwon, Nandy, & Tjan, 2013). This may not be the best idea because long-distance saccades are required to view the targets on the opposite side of the central scotoma. Moreover, PRL-based saccades tend to block the targets with the central scotoma (White & Bedell, 1990; Whittaker, Cummings, & Swieson, 1991) because the old foveating habits cannot be abandoned easily. Our results showed that the same number of trials can produce similar learning effects at multiple orientation and location conditions versus at a single condition (Figure 1). There was also an additional benefit of learning being unspecific. These findings suggest the feasibility of training a preferred retinal annulus (PRA) around the scotoma without much extra efforts. The patients would learn to use the nearest part of the PRA to make shorter and more precise saccades to view a peripheral target, and the eye movements would still be fovea based. Such a PRA training strategy may dramatically speed up the vision training for patients with central scotoma, as supported by our preliminary data in observers with artificial scotoma (Xie, Liu, & Yu, 2018).

Keywords: perceptual learning, orientation, abstraction



This research was supported by Natural Science Foundation of China Grant 31230030.

- paradigm to improve vision in patients with central scotoma. *Journal of Vision*, 18, 1067.
- Xie, X. Y., & Yu, C. (2019). Perceptual learning of Vernier discrimination transfers from high to zero noise after double training. *Vision Research*, 156, 39–45.
- Xiong, Y. Z., Tan, D. L., Zhang, Y. X., & Yu, C. (2019). Complete cross-frequency transfer of tone frequency learning after double training. *Journal of Experimental Psychology: General*, 149, 94–103.
- Xiong, Y. Z., Zhang, J. Y., & Yu, C. (2016). Bottom-up and top-down influences at untrained conditions determine perceptual learning specificity and transfer. *Elife*, 5, 14614.
- 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.
- Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, 4, 169–182.
- Zhang, J. Y., Cong, L. J., Klein, S. A., Levi, D. M., & Yu, C. (2014). Perceptual learning improves adult amblyopic vision through rule-based cognitive compensation. *Investigative Ophthalmology & Visual Science*, 55, 2020–2030.
- Zhang, J. Y., Kuai, S. G., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2008). Stimulus coding rules for perceptual learning. *PLoS Biology*, 6, 1651–1660.
- 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.