Broad bandwidth of perceptual learning in second-order contrast modulation detection

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Comparing characteristics of learning in first- and second-order systems might inform us about different neural plasticity in the two systems. In the current study, we aim to determine the properties of perceptual learning in second-order contrast modulation detection in normal adults. We trained nine observers to detect second-order gratings at an envelope modulation spatial frequency of 8 cycles/° with their nondominant eyes. We found that, although training generated the largest improvements around the trained frequency, contrast sensitivity over a broad range of spatial frequencies also improved, with a 4.09-octave bandwidth of perceptual learning, exhibiting specificity to the trained spatial frequency as well as a relatively large degree of generalization. The improvements in the modulation sensitivity function (MSF) were not significantly different between the trained and untrained eyes. Furthermore, training did not significantly change subjects' ability in detecting first-order gratings. Our results suggest that perceptual learning in second-order detection might occur at the postchannel level in binocular neurons, possibly through reducing the internal noise of the visual system.

Introduction

It is widely accepted that perceptual learning can generate long-lasting visual performance improvements in adults. Such training-induced plasticity has been established in a variety of visual tasks, ranging from simple luminance-contrast detection (Huang, Zhou, & Lu, 2008; Sowden, Rose, & Davies, 2002; Zhou et al., 2006), orientation identification (Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992), motion detection (Hou et al., 2011; Huang, Lu, Tjan, Zhou, & Liu, 2007; Watanabe, Náñez, & Sasaki, 2001), spatial frequency

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learning (Astle, Webb, & McGraw, 2010), and direction discrimination (Ball & Sekuler, 1987; Liu & Vaina, 1998), to more complex tasks such as texture discrimination (Karni & Sagi, 1991), contour judgment (McKendrick & Battista, 2013; Rubin, Nakayama, & Shapley, 1997), face identification (Gold, Bennett, & Sekuler, 1999), and video game playing (Green & Bavelier, 2003; Li et al., 2013; Li, Ngo, Nguyen, & Levi, 2011).

In most of these studies, the stimuli are defined by luminance variations that are processed by the first-order system through spatiotemporal frequency channels in the primary visual cortex (Campbell & Robson, 1968; Shapley & Lennie, 1985). Visual stimuli can also be defined by feature variations, such as contrast (Dakin & Mareschal, 2000; Schofield & Georgeson, 2003), texture (Cavanagh & Mather, 1989; Regan, 2000; Sutter & Graham, 1995; Werkhoven, Sperling, & Chubb, 1993), and orientation (Larsson, Landy, & Heeger, 2006) modulations that are processed by the second-order system (Chubb & Sperling, 1989; Lu & Sperling, 1995) through initial linear filtering, rectification, and second-stage linear filters (Baker, 1999; Chubb & Sperling, 1988, 1989; Wilson, 1999). The initial linear-filter stage of second-order processing is usually associated with cortical processing in V1; the second linear-filter stage is usually associated with cortical processing in V2 or higher-level cortical areas (Lin & Wilson, 1996). A number of psychophysical and physiological studies have provided evidence for the existence of dedicated pathways for first-order and second-order processing (Lu & Sperling, 1995, 2001; McGraw, Levi, & Whitaker, 1999; Nishida, Ledgeway, & Edwards, 1997; Schofield & Georgeson, 1999; Vaina, Cowey, & Kennedy, 1999, but see Allard & Faubert, 2013; Johnston, McOwan, & Buxton, 1992).

Although several studies have evaluated the properties of perceptual learning with high-order stimuli (Chung, Li, & Levi, 2008; Dosher & Lu, 2006; McGovern, Webb, & Peirce, 2012; Petrov & Hayes, 2010; Vaina & Chubb, 2012; Zanker, 1999), the proposed models of first-order and second-order processing provide a valuable framework to test the level(s) of learning-induced plasticity. If perceptual learning only occurs in first-order tasks or occurs for both first- and second-order tasks but with different properties, it would imply different plasticity in the two processing systems and provide evidence for learning at different levels of the visual pathway. For example, McGovern et al. (2012) found learning to discriminate orientation can benefit performance on the curvature task, but less on a global-form task, whereas learning with a global-form task can generalize to a curvature task but less on the orientation task. Zanker (1999) trained observers with both phi-motion (first-order) and theta-motion (third-order). He found that whereas learning in theta-motion largely transferred to phi-motion, learning in phi-motion didn't benefit perception of theta-motion, suggesting the engagement of at least partially distinct perceptual learning processes in first- and third-order motion. Dosher and Lu (2006) found that learning was evident in second-order texture-defined letter identification in low levels of external noise but not in high levels of external noise, and was almost absent in first-order letter identification. Petrov and Hayes (2010) investigated perceptual learning with luminance-modulated (first-order) and contrast-modulated (second-order) stimuli. Consistent with Zanker (1999), they found that the learning effect fully transferred from second-order to first-order motion but not vice versa (Petrov & Hayes, 2010). On the other hand, Chung, Li, and Levi (2008) trained observers with amblyopic vision to identify near-threshold luminance-defined (first-order) and contrast-defined (second-order) letters and found that the learning effect transferred from first-order to second-order tasks but not vice versa. Vaina and Chubb (2012) found no transfer between perceptual learning of luminance-defined (first-order) global motion and texture-contrast–defined (second-order) global motion tasks. Although the results on transfer of perceptual learning between first- and second-order processing are mixed, these previous studies suggest that first- and second-order perceptual learning might be at least partially independent.

The aim of the current study is to characterize the bandwidth and eye-specificity of perceptual learning in second-order contrast-modulation detection and its impact on first-order grating detection. Two previous studies on first-order grating detection found that the effect of learning was largely specific to the trained spatial frequency and trained eye in both fovea (Huang et al., 2008) and periphery (Sowden et al., 2002). To our best knowledge, no study has evaluated these properties in second-order perceptual learning. Here, we measured the magnitude of perceptual learning in second-order contrast-modulation detection and evaluated transfer of learning to the untrained eye, untrained spatial frequencies, and a first-order grating-contrast detection task. We compared the characteristics of perceptual learning in second-order contrast-modulation detection to published results on first-order grating detection to gain insights into neural plasticity at different levels of visual processing.

Materials and methods

Observers

Seventeen observers were assigned to the training ($N = 9$, 21–23 years) and control ($N = 8$, 21–28 years)

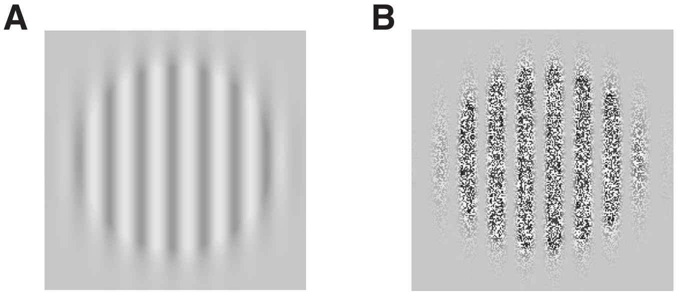

Figure 1. Illustration of the first-order (A) and second-order (B) stimuli.

groups. All observers were naive to the purpose of the study and had no prior experience in psychophysical tasks. Written informed consent was obtained from each observer before the beginning of the study, which was approved by the Institutional Review Board of the University of Science and Technology of China and the Institute of Psychology, Chinese Academy of Sciences.

Apparatus

All experiments were controlled by a PC computer running Matlab programs with Version 2.54 of Psychtoolbox extensions (Brainard, 1997; Pelli, 1997). Observers, seated with head placed on a chin rest, viewed all the stimuli on a gamma-corrected Sony G220 monitor (Sony, Tokyo, Japan) with 1024 × 768-pixel resolution and 100-Hz frame rate in a dark room. A videoSwitcher (http://lobes.osu.edu/videoSwitcher/) was used to combine analog video signals from the red and blue channels of the computer graphics cards (model Quadro 2000, Nvidia, Santa Clara, CA) with different weights using a passive resister network (Pelli & Zhang, 1991) and an active circuit to deliver identical video signals to the three channels of the color monitor and produce a 14-bit gray-level resolution (Li & Lu, 2012; Li, Lu, Xu, Jin, & Zhou, 2003).

Stimuli

Two kinds of stimuli were used in the study: first-order, luminance-defined vertical sine wave gratings (Figure 1A) and second-order, contrast-modulated noise (Figure 1B). The carrier of the second-order stimuli consisted of binary noise elements with check size of 0.1° × 0.1° and contrast of 50%. The modulators were vertical sine waves of various spatial frequencies. All stimuli were viewed monocularly at fovea with a 3.53-m viewing distance, subtending a 2.4° × 2.4° area. To minimize edge effects, a 0.45° wide half-Gaussian ramp was added to the edges of the stimuli to blend them to the background.

Design

The study consisted of four consecutive stages: a pretraining practice stage, a pretraining test stage, a monocular training stage, and a posttraining test stage. All observers were trained in their nondominant eyes.

In the pretraining practice stage, observers performed 600–700 practice trials of the first-order and second-order detection tasks that covered all the spatial frequencies. In the pre- and posttraining test stages, modulation sensitivity functions (MSFs) in second-order contrast-modulation detection were measured in monocular vision for both eyes. In addition, the contrast sensitivity function (CSF) in first-order sine wave grating detection was measured in the trained eye. Modulation sensitivity, defined as the reciprocal of modulation threshold at 79.4% correct in second-order contrast-modulation detection, was measured at six modulation spatial frequencies (0.5, 1, 2, 4, 8, and 10 cycles/° in the training group and 1, 2, 4, 8, 12, and 16 cycles/° in the control group) in the second-order task. Note that the slightly different spatial frequencies were tested in the control group. Contrast sensitivity, defined as the reciprocal of contrast threshold at 79.4% correct in first-order grating detection, was measured at seven spatial frequencies (1, 2, 4, 8, 16, 24, and 32 cycles/°). A miniblock design was used to measure the MSFs and CSFs. Each MSF was measured using 24 miniblocks of 25 trials each; each CSF was measured with 28 miniblocks. Each miniblock contained stimuli of only one spatial frequency, and was preceded by a high contrast demo of the signal in the miniblock. The order of spatial frequency conditions across miniblocks was random. Observers could take an optional rest when they finished every 100 trials. The testing sequence of the two MSFs and one CSF was counterbalanced across observers.

In the training stage, observers practiced in a second-order contrast modulation detection task using their nondominant eye. The modulation spatial frequency of the second-order gratings was fixed at 8 cycles/°. A three-down one-up staircase procedure, with a step size equal to 10% of the current modulation depth of the stimulus, was used to track observers' threshold at 79.4% accuracy. Each observer was trained for 10 sessions on separate days, with 720 trials per session. Observers were allowed to take an optional break when they finished every 120 trials.

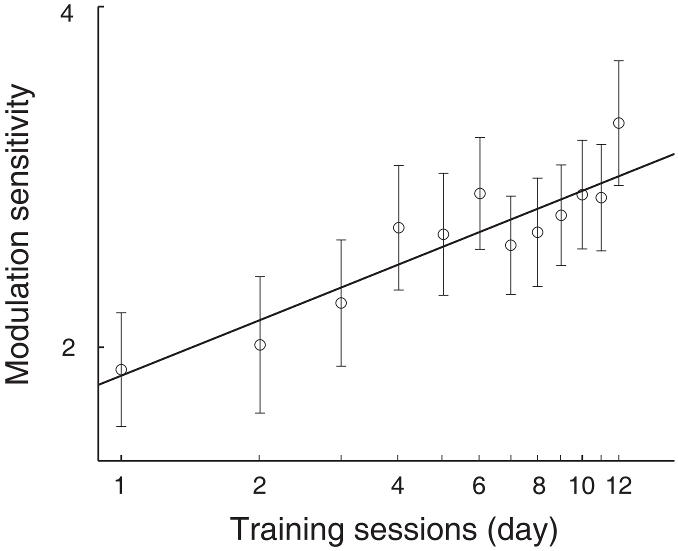

Figure 2. Average learning curve of nine observers. The first and last points were derived from the pre- and posttraining measurements of MSF, respectively. The solid line represents linear regression with a slope of 0.16, explaining 83% of the variance ($p < 0.0001$). Error bars stand for *SEM*.

Procedure

A two-interval forced-choice procedure was used in all the measurements. A typical presentation sequence in each trial consisted of a 420-ms fixation cross signalled by a brief tone in the end, the first stimulus interval, a 420-ms interstimulus interval (ISI) signalled by a brief tone in the end, the second stimulus interval, and a blank screen until response. In the first-order grating-detection task, each stimulus interval lasted 100 ms; a first-order grating was only presented in one of the two randomly chosen intervals, with no stimulus in the other interval. In the second-order contrast-modulation detection task, each interval lasted 300 ms; a second-order contrast-modulation stimulus was presented in one of the two randomly chosen intervals; the other interval contained only carrier noise (no modulation). The observer responded with a key press to indicate if the grating was presented in the first or second interval. The next trial started immediately after the response.

Data analysis

Post- and pretraining MSFs and CSFs were compared using within-subject analysis of variance (ANOVA). Post- and pretraining performance at the trained spatial frequency was compared using two-tailed paired *t* tests. The magnitude of modulation sensitivity improvements in the two eyes across the six tested spatial frequencies was compared using within-subject ANOVA.

Improvement in contrast sensitivity at the trained spatial frequency was defined as:

$$I = 20\times\log_{10}\left(\frac{\text{Post\_measure}}{\text{Pre\_measure}}\right)dB. \tag{1}$$

The pretraining MSFs and CSFs were fitted with a double-parabolic function; the posttraining MSFs and CSFs were fitted by adding a Gaussian function to each pretraining parabolic function to model the improvements in modulation and contrast sensitivities. The bandwidth of perceptual learning was then derived from the standard deviation of the Gaussian function (Huang et al., 2008).

Results

Observers were trained in a monocular 8 cycles/° second-order contrast-modulation detection task in their nondominant eye for ten days. Prior to and after training, MSFs in second-order contrast-modulation detection were measured in monocular vision for both eyes. In addition, CSF in first-order sinewave grating detection was measured in the trained eye.

Improvements at the trained modulation spatial frequency

Training in monocular second-order contrast modulation resulted in significant modulation sensitivity improvements at the trained frequency, $t(8) = 4.89$, $p = 0.001$, two-tailed. The average improvement was 4.34 ± 0.89 dB (*SEM*, same in the rest of the paper). The average learning curve is shown in Figure 2. Taking the pre- and posttraining measurements of second-order modulation sensitivity into account, training improved contrast modulation sensitivity (MS, the reciprocal of the detection threshold) by an average of 0.16 log units per log session ($r^2 = 0.83$, $p < 0.0001$).

Bandwidth of perceptual learning

Although training took place in a single modulation spatial frequency, measurements of the second-order MSF before and after training enabled us to determine performance improvements in a wide range of spatial frequencies. As shown in Figure 3, training at a single modulation frequency of 8 cycles/° induced a significant improvement of the entire MSF. Averaged over observers and spatial frequencies, MS improved by 2.57 ± 0.33 dB. A within-subject ANOVA revealed that

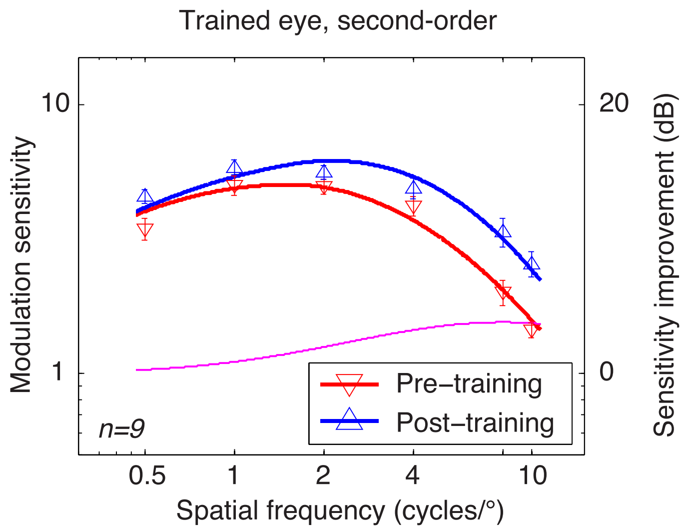

Figure 3. The average MSFs before and after training (thick red and blue lines; left ordinate) and the difference between the best-fitting post- and pretraining MSFs (thin purple line; right ordinate) in the trained eye. ▼ symbols represent the pretraining performance; ▲ symbols represent the posttraining performance. Error bars, *SEM*. The pretraining MSF was fitted with a double-parabolic function, and the posttraining MSF was fitted by adding a Gaussian function that resembles learning-induced improvements to the best-fitting pretraining function.

modulation sensitivity varied significantly with both spatial frequency, $F(5, 40) = 50.57$, $p < 0.0001$, and training, $F(1, 8) = 24.88$, $p = 0.001$, with no significant interaction, $F(5, 40) = 1.18$, $p = 0.33$. The results suggest a relatively broad transfer of learning across spatial frequencies.

Subtracting the pretraining MSF from the posttraining MSF allowed us to evaluate transfer of perceptual learning at 8 cycles/° to other untrained spatial frequencies and estimate the bandwidth of perceptual learning in second-order modulation detection. The average improvement curve is shown in Figure 3 as a thin purple line. The bandwidth of the improvement curve is 4.09 octaves, which is significantly broader than both the typical 1–2 octave channel bandwidth in second-order processing (Arsenault & Wilkinson, 1999; Reynaud & Hess, 2012; Westrick, Henry, & Landy, 2013) and the reported 1–2 octaves bandwidth of perceptual learning in first-order grating detection (Huang et al., 2008; Sowden et al., 2002; Zhou et al., 2006).

Improvement of the MSF in the untrained eye

The pre- and posttraining MSFs in the untrained eye are shown in Figure 4. Obviously, learning transferred significantly to the untrained eye. Modulation sensitivity at 8 cycles/° (i.e., the trained frequency) in the untrained eye improved by 3.21 ± 1.32 dB following training, $t(8) = 2.93$, $p = 0.019$, two-tailed, which was not significantly different from that in the trained eye, $t(8) = -0.525$, $p = 0.614$, two-tailed. Averaged across observers and spatial frequencies, MS improved 1.54 ± 0.41 dB. A within-subject ANOVA also revealed that MS varied significantly with both spatial frequency, $F(5, 40) = 27.79$, $p < 0.0001$, and training, $F(1, 8) = 5.92$, $p = 0.041$, with no significant interaction, $F(5, 40) = 1.01$, $p = 0.42$. The bandwidth of the improvement curve (purple line in Figure 4) is 3.88 octaves. The average magnitude of modulation sensitivity improvement across all the spatial frequencies in the trained eye did not differ significantly from that in the untrained eye, $F(1, 16) = 1.63$, $p = 0.22$.

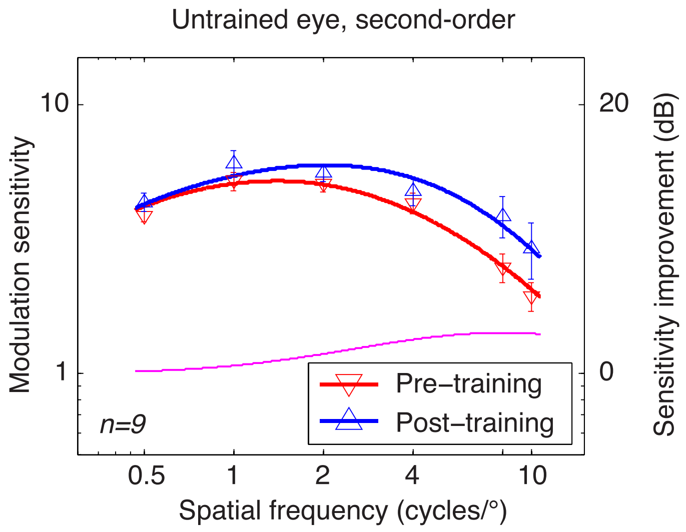

Figure 4. Average MSFs before and after training in the untrained eye. ▼ symbols represent the pretraining performance; ▲ symbols represent the posttraining performance. Error bars, *SEM*. The solid lines represent curves fitted with a double-parabola function (pretraining MSF) and a double-parabola plus Gaussian function (posttraining). See Materials and methods for details.

Improvement in the untrained first-order detection task

To evaluate transfer of perceptual learning in the second-order system to the first-order system, we obtained pre- and posttraining contrast sensitivity functions in the trained eye (Figure 5). Clearly, training in second-order contrast-modulation detection didn't generate any significant improvement in first-order grating detection, $F(1, 8) = 0.028$, $p = 0.87$. The average magnitude of improvement in contrast sensitivity across observers and spatial frequencies was 0.40 ± 0.32 dB.

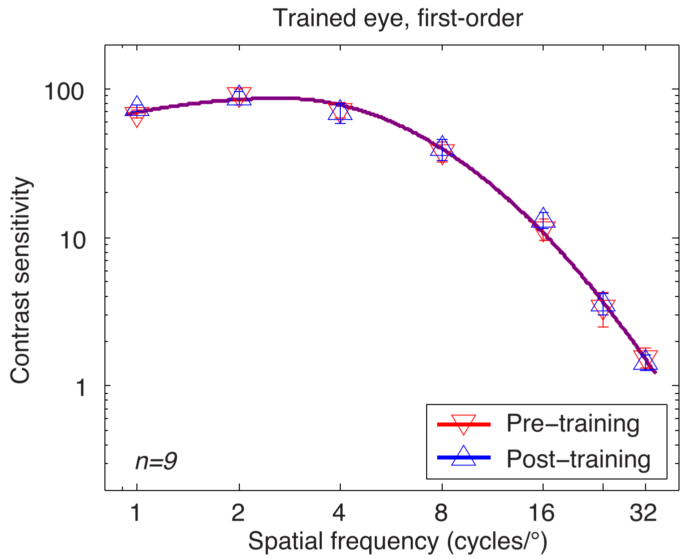

Figure 5. Average contrast sensitivity functions before and after training in the trained eye. ▼ symbols represent the pretraining performance; ▲ symbols represent the posttraining performance. Error bars, *SEM*. The solid lines represent curves fitted with a double-parabola function.

Performance of the control group

To rule out the possibility that improvement in second-order contrast-modulation detection is due to repeated tests, we also conducted a control experiment in which observers received no training but the same pre- and posttraining measurements as the training group (same measurements, i.e., MSF of two eyes and CSF of the nondominant eye and same time gap of 10 days between the two sessions). The average MSF of the nondominant eye, the average MSF of the dominant eye, and the average CSF of the nondominant eye are plotted in Figure 6A through C, respectively. Obviously, test–retest did not produce any significant improvement in any of these measures (all $p > 0.5$). The average magnitude of improvement in modulation sensitivity across observers and spatial frequencies was 0.18 ± 3.23 dB, −0.46 ± 3.38 dB, and 1.48 ± 3.45 dB for second-order detection in the nondominant eye, second-order detection in the dominant eye, and first-order detection in the nondominant eye, respectively.

Discussion

In the current study, we investigated the specificity and generalizability of perceptual learning in second-order contrast-modulation detection. We show that training in second-order contrast-modulation detection in a fixed spatial frequency in the nondominant eye significantly improved modulation sensitivity at the trained spatial frequency (4.34 dB). Training also increased modulation sensitivity over a wide range of spatial frequencies in the trained eye (average improvement of 2.57 dB; learning bandwidth: 4.09 octaves) and the untrained eye (average improvement of 1.54 dB; learning bandwidth: 3.88 octaves), with no significant difference between the improvements in the two eyes. In addition, we found that training in second-order contrast-modulation detection did not benefit performance in first-order grating detection.

In our study, white noise was used as a carrier for the second-order stimuli. Due to black-white asymmetry in visual processing (Lu & Sperling, 2012; Schofield & Georgeson, 2003), such stimuli may potentially contain first-order luminance contaminations. A detailed analysis based on the estimated magnitude of black-white asymmetry for comparable stimuli in Lu and Sperling (2012) revealed that first-order contamination in our second-order stimuli in all the tested spatial frequencies was much lower than the subject's contrast detection threshold; subjects had to rely on second-order mechanisms to perform the second-order contrast-modulation detection task. Any learning observed in second-order contrast-modulation detection should have resulted from learning in the second-order system. The finding that there is no significant improvement of first-order CSF before and after training in second-order contrast-modulation detection provided further support.

In this study, the pretraining modulation sensitivity was about 2.0 at the training modulation frequency (8 cycles/°). A similar procedure was also used to select training frequency in studying perceptual learning in first-order grating detection in several earlier publications (Huang et al., 2008; Zhou et al., 2012; Zhou et al., 2006) in which the cutoff spatial frequency of the contrast-sensitivity function (sensitivity = 2.0) was used as the training frequency. Because cutoff frequencies and similar amount of practice have been used in both first- and second-order training, we can compare the magnitude of improvements in their respective cutoff frequency: second-order detection, 4.34 dB (current study); first-order detection, 5.6 dB (Huang et al., 2008); first-order detection with high-order optical-aberration correction, 5.39 dB; and first-order detection without high-order optical-aberration correction: 3.42 dB (Zhou et al., 2012). So the magnitudes of learning effects are comparable in first- and second-order detection at their respective cutoff spatial frequencies.

It has been established that perceptual learning in first-order contrast detection is largely spatial frequency specific, with a 1–2 octaves bandwidth of learning in both fovea (Huang et al., 2008; Zhou et al., 2012) and periphery (Sowden et al., 2002), and comparable to the estimated bandwidth of first-order spatial frequency channels (Stromeyer & Klein, 1974). In this paper, we

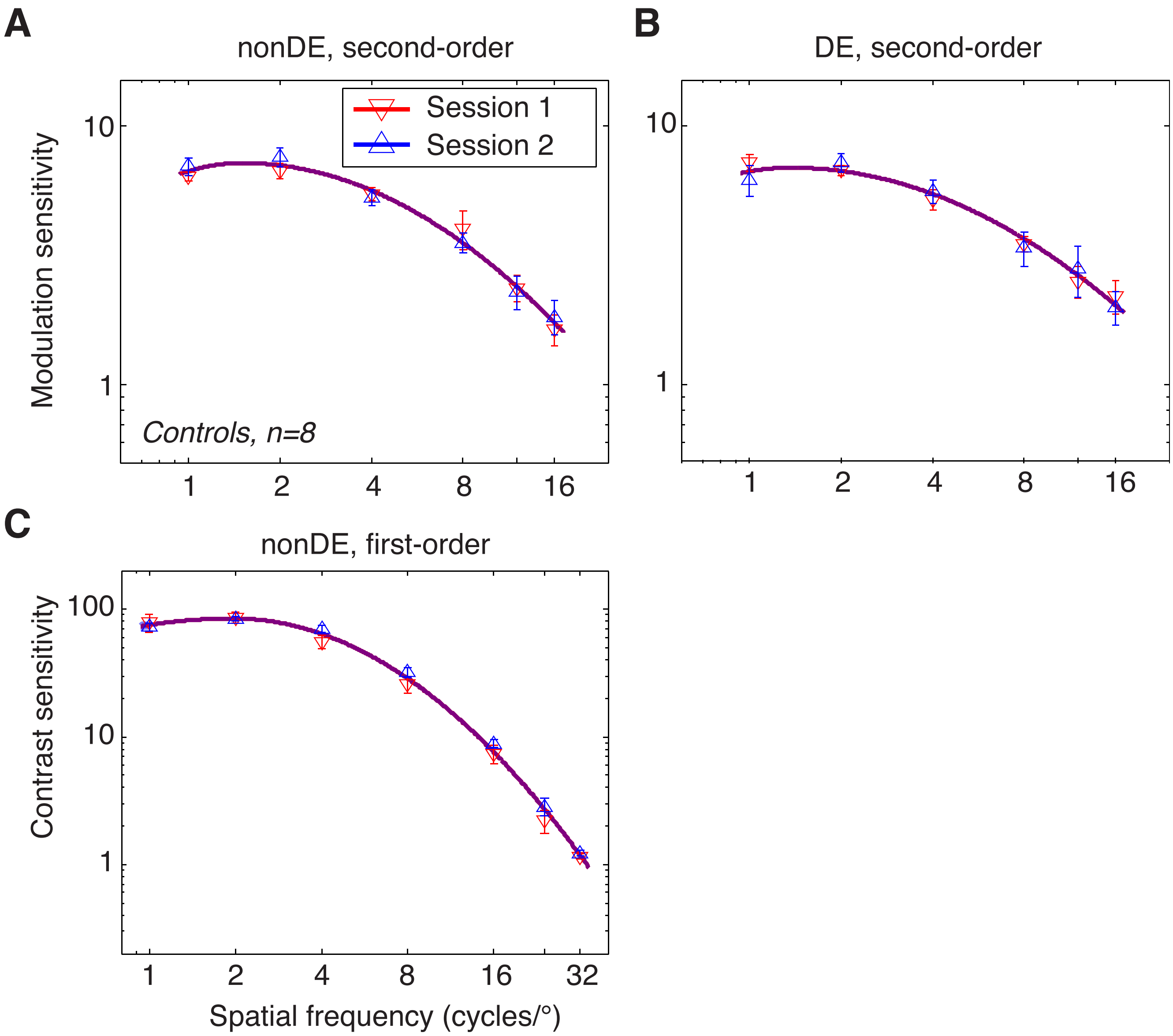

Figure 6. Performance of the control group. DE, dominant eye; nonDE: nondominant eye. Error bars, *SEM*. The solid lines represent the best fitting double-parabola function.

found that the bandwidth of perceptual learning (4.09 octaves) in second-order contrast-modulation detection was much broader than that in first-order grating detection and the estimated spatial channel bandwidth of the second-order system (1–2 octaves; Arsenault & Wilkinson, 1999; Reynaud & Hess, 2012; Westrick et al., 2013). These results suggest that perceptual learning of the second-order stimuli, unlike that of the first-order stimuli, is not channel-specific and can generalize across spatial frequency channels. On the other hand, we also show that the learning effect is specific to second-order processing. This result, together with previously reported asymmetry of transfer of learning between first- and second-order stimuli (Chen, Qiu, Zhang, & Zhou, 2009; Chung et al., 2008; Petrov & Hayes, 2010; Vaina & Chubb, 2012), indicates that perceptual learning in first- and second-order processing may occur at different stages of visual processing.

Current theories on perceptual learning have attempted to interpret the mechanism of training-induced plasticity with reduction of internal noise and/or retuning of the perceptual template (Dosher & Lu, 1998; Li, Levi, & Klein, 2004; Lu & Dosher, 2004; Petrov, Dosher, & Lu, 2005). Previous studies on perceptual learning of first-order stimuli have shown that for observers with high internal noise (e.g., amblyopes; Huang, Tao, Zhou, & Lu, 2007; Xu, Lu, Qiu, & Zhou, 2006), training at one spatial frequency induced broad transfer to untrained spatial frequencies (Huang et al., 2008) through reduction of the high internal noise in the amblyopic visual system (Huang, Lu, & Zhou, 2009). There is evidence that the visual system has higher internal noise in detecting second-order stimuli than in detecting the first-order stimuli (Allard & Faubert, 2006). It is quite possible that training with second-order stimuli detection may decrease postchannel internal noise and therefore induce broad transfer across frequencies (Dosher & Lu, 2006). The finding that perceptual learning in second-order processing was not specific to the trained eye suggests that such learning may occur after binocular combination, consistent with the hypothesis that perceptual learning in second-order detection might reduce the internal noise of the visual system at the postchannel level.

We conclude that training in second-order detection could generate large improvements at the trained frequency, and the learning effect is specific to second-order processing, but not to the trained modulation frequency and eye. Perceptual learning of second-order detection might occur in binocular neurons, possibly through internal noise reduction.

Keywords: second-order modulation detection, perceptual learning, modulation sensitivity, generalizability, specificity

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References

Allard, R., & Faubert, J. (2006). Same calculation efficiency but different internal noise for luminance- and contrast-modulated stimuli detection. *Journal of Vision*, *6*(4):3, 322–334, http://www.journalofvision.org/content/6/4/3, doi:10.1167/6.4.3. [PubMed] [Article]

Allard, R., & Faubert, J. (2013). No dedicated second-order motion system in the periphery. *Journal of Vision*, *13*(9):766, http://www.journalofvision.org/content/13/9/766, doi:10.1167/13.9.766. [Abstract]

Arsenault, A. S., & Wilkinson, F. (1999). Modulation frequency and orientation tuning of second-order texture mechanisms. *Journal of the Optical Society of America A*, *16*(3), 427–435.

Astle, A. T., Webb, B. S., & McGraw, P. V. (2010). Spatial frequency discrimination learning in normal and developmentally impaired human vision. *Vision Research*, *50*(23), 2445–2454.

Baker, C. L., Jr. (1999). Central neural mechanisms for detecting second-order motion. *Current Opinion in Neurobiology*, *9*(4), 461–466.

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*(4), 433–436.

Campbell, F. W., & Robson, J. (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology*, *197*(3), 551–566.

Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision*, *4*, 103–129.

Chen, R., Qiu, Z. P., Zhang, Y., & Zhou, Y. F. (2009). Perceptual learning and transfer study of first- and second-order motion direction discrimination. *Progress in Biochemistry & Biophysics*, *36*(11), 1442–1450.

Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, *5*(11), 1986–2007.

Chubb, C., & Sperling, G. (1989). Two motion perception mechanisms revealed through distance-driven reversal of apparent motion. *Proceedings of the National Academy of Sciences*, *86*(8), 2985–2989.

Chung, S. T., Li, R. W., & Levi, D. M. (2008). Learning to identify near-threshold luminance-defined and contrast-defined letters in observers with amblyopia. *Vision Research*, *48*(27), 2739–2750.

Dakin, S. C., & Mareschal, I. (2000). Sensitivity to contrast modulation depends on carrier spatial frequency and orientation. *Vision Research*, *40*(3), 311–329.

Dosher, B. A., & Lu, Z.-L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences*, *95*(23), 13988–13993.

Dosher, B. A., & Lu, Z.-L. (2006). Level and mechanisms of perceptual learning: Learning first-order luminance and second-order texture objects. *Vision Research*, *46*(12), 1996–2007.

Gold, J., Bennett, P., & Sekuler, A. (1999). Signal but not noise changes with perceptual learning. *Nature*, *402*(6758), 176–178.

Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature*, *423*(6939), 534–537.

Hou, F., Huang, C.-B., Tao, L., Feng, L., Zhou, Y., & Lu, Z.-L. (2011). Training in contrast detection improves motion perception of sinewave gratings in amblyopia. *Investigative Ophthalmology & Visual Science*, *52*(9), 6501–6510, http://www.iovs.org/content/52/9/6501. [PubMed] [Article]

Huang, C.-B., Lu, Z.-L., & Zhou, Y. (2009). Mechanisms underlying perceptual learning of contrast detection in adults with anisometropic amblyopia. *Journal of Vision*, *9*(11):24, 1–14, http://www.journalofvision.org/content/9/11/24, doi:10.1167/9.11.24. [PubMed] [Article]

Huang, C.-B., Tao, L., Zhou, Y., & Lu, Z.-L. (2007). Treated amblyopes remain deficient in spatial vision: A contrast sensitivity and external noise study. *Vision Research*, *47*(1), 22–34.

Huang, C.-B., Zhou, Y., & Lu, Z.-L. (2008). Broad bandwidth of perceptual learning in the visual system of adults with anisometropic amblyopia. *Proceedings of the National Academy of Sciences*, *105*(10), 4068–4073.

Huang, X., Lu, H., Tjan, B. S., Zhou, Y., & Liu, Z. (2007). Motion perceptual learning: When only task-relevant information is learned. *Journal of Vision*, *7*(10):14, 1–10, http://www.journalofvision.org/content/7/10/14, doi:10.1167/7.10.14. [PubMed] [Article]

Johnston, A., McOwan, P., & Buxton, H. (1992). A computational model of the analysis of some first-order and second-order motion patterns by simple and complex cells. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *250*(1329), 297–306.

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

Larsson, J., Landy, M. S., & Heeger, D. J. (2006). Orientation-selective adaptation to first- and second-order patterns in human visual cortex. *Journal of Neurophysiology*, *95*(2), 862–881.

Li, J., Thompson, B., Deng, D., Chan, L. Y., Yu, M., & Hess, R. F. (2013). Dichoptic training enables the adult amblyopic brain to learn. *Current Biology*, *23*(8), R308–R309.

Li, R. W., Levi, D. M., & Klein, S. A. (2004). Perceptual learning improves efficiency by re-tuning the decision 'template' for position discrimination. *Nature Neuroscience*, *7*(2), 178–183.

Li, R. W., Ngo, C., Nguyen, J., & Levi, D. M. (2011). Video-game play induces plasticity in the visual system of adults with amblyopia. *PLoS Biology*, *9*(8), e1001135.

Li, X., & Lu, Z.-L. (2012). Enabling high grayscale resolution displays and accurate response time measurements on conventional computers. *Journal of Visualized Experiments*, *60*, 3312.

Li, X., Lu, Z.-L., Xu, P., Jin, J., & Zhou, Y. (2003). Generating high gray-level resolution monochrome displays with conventional computer graphics cards and color monitors. *Journal of Neuroscience Methods*, *130*(1), 9–18.

Lin, L.-M., & Wilson, H. R. (1996). Fourier and non-Fourier pattern discrimination compared. *Vision Research*, *36*(13), 1907–1918.

Liu, Z., & Vaina, L. M. (1998). Simultaneous learning of motion discrimination in two directions. *Cognitive Brain Research*, *6*(4), 347–349.

Lu, Z.-L., & Dosher, B. A. (2004). Perceptual learning retunes the perceptual template in foveal orientation identification. *Journal of Vision*, *4*(1):5, 44–56, http://www.journalofvision.org/content/4/1/5, doi:10.1167/4.1.5. [PubMed] [Article]

Lu, Z.-L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, *35*(19), 2697–2722.

Lu, Z.-L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: Review and update. *Journal of the Optical Society of America A: Optics, Image Science, & Vision*, *18*(9), 2331–2370.

Lu, Z.-L., & Sperling, G. (2012). Black-white asymmetry in visual perception. *Journal of Vision*, *12*(10):8, 1–21, http://www.journalofvision.org/content/12/10/8, doi:10.1167/12.10.8.

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

McGraw, P. V., Levi, D. M., & Whitaker, D. (1999). Spatial characteristics of the second-order visual pathway revealed by positional adaptation. *Nature Neuroscience*, *2*(5), 479–484.

McKendrick, A. M., & Battista, J. (2013). Perceptual learning of contour integration is not compromised in the elderly. *Journal of Vision*, *13*(1):5, 1–10, http://www.journalofvision.org/content/13/1/5, doi:10.1167/13.1.5. [PubMed] [Article]

Nishida, S., Ledgeway, T., & Edwards, M. (1997). Dual multiple-scale processing for motion in the human visual system. *Vision Research*, *37*(19), 2685–2698.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, *31*(7–8), 1337–1350.

Petrov, A. A., Dosher, B. A., & Lu, Z.-L. (2005). The dynamics of perceptual learning: An incremental reweighting model. *Psychological Review*, *112*(4), 715–743.

Petrov, A. A., & Hayes, T. R. (2010). Asymmetric transfer of perceptual learning of luminance-and contrast-modulated motion. *Journal of Vision*, *10*(14):11, 1–22, http://www.journalofvision.org/content/10/14/11, doi:10.1167/10.14.11. [PubMed] [Article]

Regan, D. (2000). *Human perception of objects: Early visual processing of spatial form defined by luminance, colour, texture, motion, and binocular disparity*. Sunderland, MA: Sinauer Associates.

Reynaud, A., & Hess, R. F. (2012). Properties of spatial channels underlying the detection of orientation-modulations. *Experimental Brain Research*, *220*(2), 135–145.

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

Schofield, A. J., & Georgeson, M. A. (1999). Sensitivity to modulations of luminance and contrast in visual white noise: Separate mechanisms with similar behaviour. *Vision Research*, *39*(16), 2697–2716.

Schofield, A. J., & Georgeson, M. A. (2003). Sensitivity to contrast modulation: The spatial frequency dependence of second-order vision. *Vision Research*, *43*(3), 243–259.

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

Shapley, R., & Lennie, P. (1985). Spatial frequency analysis in the visual system. *Annual Review of Neuroscience*, *8*(1), 547–581.

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

Sowden, P. T., Rose, D., & Davies, I. R. (2002). Perceptual learning of luminance contrast detection: Specific for spatial frequency and retinal location but not orientation. *Vision Research*, *42*(10), 1249–1258.

Stromeyer, C., III, & Klein, S. (1974). Spatial frequency channels in human vision as asymmetric (edge) mechanisms. *Vision Research*, *14*(12), 1409–1420.

Sutter, A., & Graham, N. (1995). Investigating simple and complex mechanisms in texture segregation using the speed-accuracy tradeoff method. *Vision Research*, *35*(20), 2825–2843.

Vaina, L. M., & Chubb, C. (2012). Dissociation of first- and second-order motion systems by perceptual learning. *Attention, Perception, & Psychophysics*, *74*(5), 1009–1019.

Vaina, L. M., Cowey, A., & Kennedy, D. (1999). Perception of first-and second-order motion: separable neurological mechanisms? *Human Brain Mapping*, *7*(1), 67–77.

Watanabe, T., Náñez, J. E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature*, *413*(6858), 844–848.

Werkhoven, P., Sperling, G., & Chubb, C. (1993). The dimensionality of texture-defined motion: A single channel theory. *Vision Research*, *33*(4), 463–485.

Westrick, Z. M., Henry, C. A., & Landy, M. S. (2013). Inconsistent channel bandwidth estimates suggest winner-take-all nonlinearity in second-order vision. *Vision Research*, *81*, 58–68.

Wilson, H. R. (1999). Non-Fourier cortical processes in texture, form, and motion perception. In P. S. Ulinski, E. G. Jones, & A. Peters (Eds.), *Models of cortical circuits* (pp. 445–477). New York: Springer.

Xu, P., Lu, Z.-L., Qiu, Z., & Zhou, Y. (2006). Identify mechanisms of amblyopia in Gabor orientation identification with external noise. *Vision Research*, *46*(21), 3748–3760.

Zanker, J. M. (1999). Perceptual learning in primary and secondary motion vision. *Vision Research*, *39*(7), 1293–1304.

Zhou, J., Zhang, Y., Dai, Y., Zhao, H., Liu, R., Hou, F., & Zhou, Y. (2012). The eye limits the brain's learning potential. *Scientific Reports*, *2*(364), 1–5.

Zhou, Y., Huang, C.-B., Xu, P., Tao, L., Qiu, Z., Li, X., & Lu, Z.-L. (2006). Perceptual learning improves contrast sensitivity and visual acuity in adults with anisometropic amblyopia. *Vision Research*, *46*(5), 739–750.