Broad bandwidth of perceptual learning in the visual system of adults with anisometropic amblyopia

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Communicated by George Sperling, University of California, Irvine, CA, January 28, 2008 (received for review December 17, 2007)

Recent studies have demonstrated that training adult amblyopes in simple visual tasks leads to significant improvements of their spatial vision. One critical question is: How much can training with one particular stimulus and task generalize to other stimuli and tasks? In this study, we estimated the bandwidth of perceptual learning in teenage and adult observers with anisometropic amblyopia and compared it to that of normal observers. We measured and compared contrast sensitivity functions—i.e., sensitivity to sine-wave gratings of various spatial frequencies—before and after training at a single spatial frequency in teenagers and adults with and without amblyopia. We found that the bandwidth of perceptual learning in the amblyopic visual system is much broader than that of the normal visual system. The broader bandwidth, suggesting more plasticity and wider generalization in the amblyopic visual system, provides a strong empirical and theoretical basis for perceptual learning as a potential treatment for amblyopia.

contrast sensitivity function | generalization | spatial vision

Amblyopia is a developmental impairment of spatial vision that affects ≈3% of the population (1). Largely a cortical disorder resulting from abnormal visual experience in early childhood, it cannot be corrected by refractive means (2). In traditional clinical practice, only young child amblyopes (<8 yr old) are treated, because of "conventional wisdom": that spatial vision, fully developed by that age, is no longer subject to therapeutic modifications (3–5). On the other hand, research in the last two decades on perceptual learning has documented remarkable plasticity in the adult visual system (6–10). These findings raise the possibility that the visual system of the adult amblyopes may still retain degrees of plasticity that can be exploited for treatment.

Attempts to use perceptual learning to treat amblyopia began with Campbell *et al*. (11) but provided mixed results in subsequent studies (12–15). The researchers in those early studies typically used high-contrast stimuli and short training periods (e.g., 7 min) that were predetermined irrespective of individual subjects' characteristics (e.g., history, type and degree of amblyopia). Later studies on perceptual learning in the normal visual system showed that it typically requires several hundreds of training trials to significantly improve performance in perceptual tasks. Several recent studies (5, 16–21) found that more elaborate training procedures on simple spatial vision tasks can lead to significant visual acuity improvements in adult amblyopes. Levi *et al*. (18, 19) found that Snellen acuities in two anisometropic amblyopes were significantly improved after intensive training in a Vernier acuity task. In addition, both Li and Levi (16) and Li *et al*. (17) showed transfer of learning of position acuity to Snellen acuity in amblyopes beyond the so-called critical period (age <8 yr). Focusing on the lack of functional spatial connections in amblyopia, Polat *et al*. (5) trained subjects to detect sine-wave gratings with collinear high-contrast flankers and gradually increased the spatial frequency of the stimulus during training. They found that training significantly improved the contrast sensitivity and visual acuity of adults with either strabismic or anisometropic amblyopia. We also observed significant improvements in contrast sensitivity and visual acuity by training adults with anisometropic amblyopia to detect sine-wave gratings at their cutoff spatial frequencies (20). In a recent publication, Chung *et al*. (21) found that the ability to detect contrast-defined letters improved in 8 of 10 (4 strabismic, 3 anisometropic, and 1 both) subjects after training. Moreover, training in contrast-defined letters also significantly benefited their performance in a luminance-defined letter identification task.

One critical concern of perceptual learning as an effective therapy for amblyopia is whether training with one particular stimulus and task generalizes to other stimuli and tasks. Although all of the studies discussed in the previous paragraph demonstrated some degree of transfer (e.g., Vernier acuity to visual acuity, position acuity to Snellen acuity), a systematic characterization of the degree of generalizability of perceptual learning in amblyopia is still critically important. This is because the hallmark of perceptual learning in the normal visual system is its high specificity to the characteristics of the training stimulus (6). If perceptual learning in the amblyopic visual system were also highly specific to the characteristics of the training stimuli and task, perceptual learning as a therapy for amblyopia would not be very effective in improving general spatial vision. At a minimum, multiple training stimuli and tasks must be used to cover the range of stimuli and tasks that are important for daily visual functions. On the other hand, perceptual learning in the amblyopic eyes that generalizes to a wide range of untrained stimuli and task conditions would provide a basis for efficient training regimens.

To evaluate and compare the generalizability of perceptual learning in amblyopic and normal vision, we estimated the bandwidth of spatial frequencies impacted by perceptual learning at a particular spatial frequency in both normals and amblyopes. Contrast sensitivity functions (CSFs)—sensitivity to sine-wave gratings of various spatial frequencies—were measured before and after perceptual learning at one spatial frequency in teenagers and adults with and without amblyopia. Direct comparisons of the post- and pretraining CSFs (Fig. 1) provides a measure of the range of spatial frequencies (the "bandwidth") impacted by perceptual learning (22). We found that the bandwidth of perceptual learning in the amblyopic visual system is much broader than that of the normal visual system.

Results

Learning Curves. For the amblyopic and normal observers in the first control group, training at the cut-off spatial frequency significantly improved contrast sensitivity ($P < 0.01$), by 10.7 dB and 5.6 dB, respectively (Fig. 2). For the observers in the second

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Author contributions: C.-B.H., Y.Z., and Z.-L.L. designed research; C.-B.H. performed research; C.-B.H. and Z.-L.L. analyzed data; and C.-B.H. and Z.-L.L. wrote the paper.

The authors declare no conflict of interest.

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www.pnas.org/cgi/doi/10.1073/pnas.0800824105

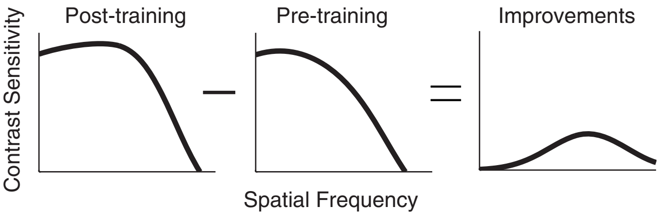

Fig. 1. Schematic diagram of the bandwidth of perceptual learning. The bandwidth of perceptual learning can be estimated by subtracting the pretraining contrast sensitivity function from the post-training contrast sensitivity function.

control group (Fig. 2), training at 10 cycles per degree of visual angle (c/°) generated a very small (0.7 dB) and nonsignificant contrast sensitivity change ($P > 0.10$). Training improved contrast sensitivity with an average rate of 10.6, 5.8, and 1.2 dB per log session, respectively, for the three groups. The magnitude of improvement was not significantly correlated with age ($r = -0.20$, $P > 0.10$).

Visual Acuity. For the amblyopic observers, training also greatly improved visual acuities in the amblyopic eyes (average: 37.2%, $P < 0.01$) and fellow eyes (13.4%, $P < 0.01$), as reported in ref. 20. No significant visual acuity improvement was observed in either control group ($P > 0.15$).

CSFs. The pre- and post-training contrast sensitivity functions in the trained eyes of all of the observers in the amblyopic and first control groups are shown in Figs. 3 and 4, respectively. In the trained eyes, significant improvements were found in the amblyopic and first control groups [$F(1,3) = 55.49$, $P < 0.01$; $F(1,13) = 14.03$, $P < 0.01$] but not in the second control group [$F(1,6) = 0.28$, $P > 0.25$]. The average magnitude of improvement across observers and spatial frequencies was 6.98, 1.49, and 0.43 dB in the three groups, respectively. Zhou *et al.* (20) previously showed that CSF improvements in the amblyopic eyes were not due to training provided by CSF assessment.

In the untrained eyes, significant improvements were found only in the amblyopic group [$F(1,8) = 8.84$, $P < 0.025$] but not in the two control groups (both $P > 0.10$). The average magnitude of improvement was 2.55, 0.21, and 0.55 dB in the three groups. Many studies have found that the fellow eyes of the amblyopes are not completely normal (23, 24). Using a second-order letter identification task, Chung *et al.* (21) also found a partial interocular transfer in adult amblyopia. The significant contrast sensitivity improvements in the untrained eyes in the amblyopic group suggest that perceptual learning in the amblyopic eyes was not at the expense of the fellow eyes.

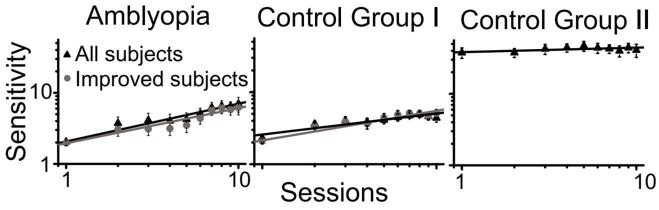

Fig. 2. Learning curves—contrast sensitivity as a function of training sessions—for the amblyopic group and two control groups. Average data from pre- and post-training CSF measurements (the first and last data points) and eight training sessions are shown. The black symbols and lines represent the average of all of the observers in each group. The gray symbols and lines represent the average of the observers who exhibited significant learning during training.

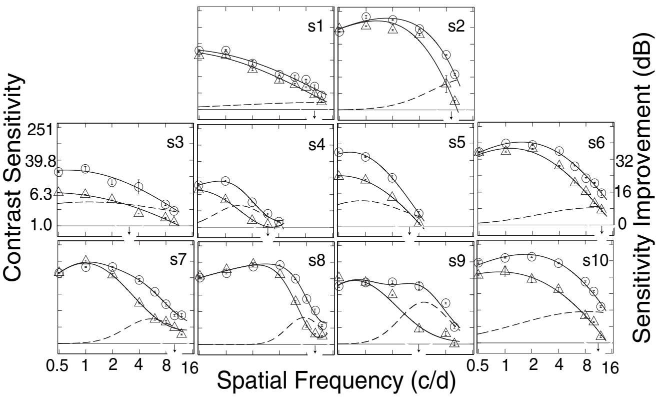

Fig. 3. Pre- and post-training contrast sensitivity functions (black symbols and curves; left ordinate) and the difference between the best fitting post- and pretraining CSFs (dashed gray curves; right ordinate) in the amblyopic eyes of the amblyopic group, subjects S1–S10. Triangles, pretraining; circles, post-training; arrows, training frequency; error bars, SEM.

Bandwidth of Perceptual Learning. To evaluate transfer of perceptual learning to other spatial frequencies, we compared the pre- and post-training contrast sensitivity functions in the trained eyes. We focused this analysis on the observers in the amblyopic group and the first control groups.[§] Only observers with significant amount of performance improvements at the training frequency, eight amblyopic and nine normal from the first control group, were included in the results reported here, although including all observers in the analysis did not significantly change the results (see *Materials and Methods*).

For the selected observers in the amblyopic and first control groups, the magnitudes of contrast sensitivity improvements at their respective training frequency were not significantly different (9.98 vs. 8.30 dB; $P > 0.25$). However, the bandwidth of perceptual learning was drastically different ($P < 0.01$): For the amblyopic observers, the average full bandwidth was 4.04 ± 0.63 octaves; the average full bandwidth was only 1.40 ± 0.30 octaves for the normal observers (Fig. 5). The mode of contrast sensitivity improvement was about 1 octave lower than the training frequency in the amblyopic group, but at the training frequency for the normal observers, consistent with the last channel theory of amblyopia (25).

Summary and Discussion

We found that, for both anisometropic amblyopes and normal observers, training in a grating detection task at their cut-off spatial frequencies improved contrast sensitivity at the training frequency. A larger fraction of the amblyopic observers (8/10) benefited from perceptual learning compared with the normal controls (9/14). For the amblyopic observers, training also improved visual acuity in the trained amblyopic eyes and contrast sensitivity function in the untrained fellow eyes. However, training normal observers at the median cut-off spatial frequency of the amblyopic eyes did not significantly improve normal observers' contrast sensitivities. Quantitative comparisons of the pre- and post-training contrast sensitivity functions revealed a 4.04-octave bandwidth of perceptual learning for the amblyopic observers, much greater than the bandwidth (1.4 octaves) for normal observers.

The observed improvement at the training spatial frequency in adults with anisometropic amblyopia are consistent with the

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[§] Three normal observers in the second control group also exhibited significant perceptual learning. Their average full bandwidth of perceptual learning at half height was 1.32 ± 0.60 octaves.

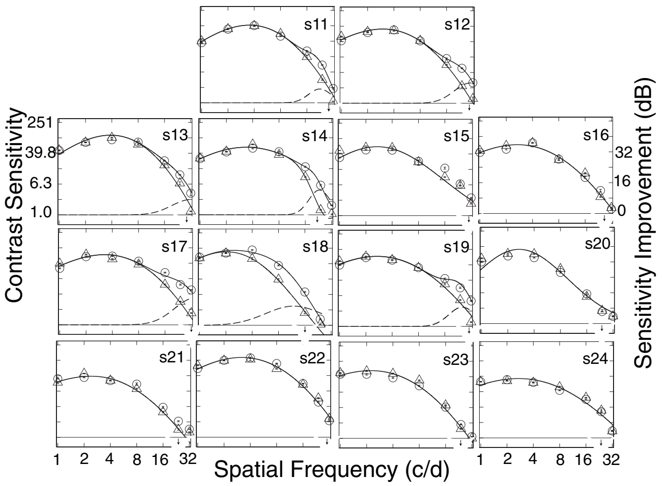

Fig. 4. Pre- and post-training contrast sensitivity functions (black symbols and curves; left ordinate) and the difference between the best fitting post- and pretraining CSFs (dashed gray curves; right ordinate) in the trained eyes of the first control group, subject S11–S24. Triangles, pretraining; circles, post-training; arrows, training frequency; error bars, SEM.

results in the literature: Zhou *et al.* (20) found an improvement of 9.8 dB in contrast sensitivity after perceptual learning at the cut-off spatial frequency; Polat *et al.* (5) found an ≈2-fold improvement in contrast sensitivity after training in a grating detection with flankers task. For the normal observers, we found significant perceptual learning after training at the cut-off (≈27 c/°) but not at a lower (10 c/°) spatial frequency. This pattern of results is consistent with many studies in the literature on normal vision that found significant perceptual learning in contrast detection *only* in noncardinal orientations (26), in parafovea (22), or in the presence of flankers (27) or large amount of external noise (28).

The method we used to quantify the bandwidth of perceptual learning was originally developed and applied to parafoveal vision of normal observers by Sowden *et al.* (22). They found that perceptual learning of contrast detection in parafovea was specific to the trained eye with a bandwidth of 1.3 octaves. Although Sowden *et al.* trained their observers at 4 c/° in parafovea and we trained our normal observers at 27 c/° in fovea, the estimated bandwidths of perceptual learning from the two independent studies are almost in perfect agreement and consistent with the typical bandwidth of spatial frequency channels (29, 30).

For amblyopic observers, the estimated bandwidth of perceptual learning is much broader than that of their spatial frequency channels, which has been estimated in sine-wave adaptation (31) and masking (32) paradigms, and an object recognition study with filtered letters (33). All these studies found that the bandwidth of the spatial frequency channels of the amblyopic visual system is virtually identical to that of the normal observers, i.e., 1–2 octaves. The estimated 4.04-octaves bandwidth of perceptual learning implies that the impact of perceptual learning generalizes across spatial frequency channels in amblyopic eyes. Such a broad bandwidth of perceptual learning may underlie the improved visual acuity in the amblyopic eyes after training, a task that involves a wide range of spatial frequencies. In contrast, the approximate equivalence of learning and channel bandwidth in normal eyes suggests that perceptual learning is channel-specific.

We used octave as the unit to measure the bandwidth of perceptual learning. If we convert the bandwidth to linear units, 4 octaves at a base frequency of 10 c/° translate into 0.625 c/° to 10 c/°; 1.4 octaves at a base frequency of 27 c/° translate into 10.2 c/° to 27 c/°. Based on this calculation, the linear bandwidth of perceptual learning of the normal eyes is wider than that of the amblyopic eyes. However, the octave unit, the conventional bandwidth metric of spatial frequency channels, reflects the underlying scale-invariant organization of spatial vision mechanisms. For our purposes, it is important to investigate whether perceptual learning generalizes to different channels. A perceptual learning effect that generalizes across spatial frequency channels is much more desirable as a therapy for amblyopia. The octave unit is thus appropriate.

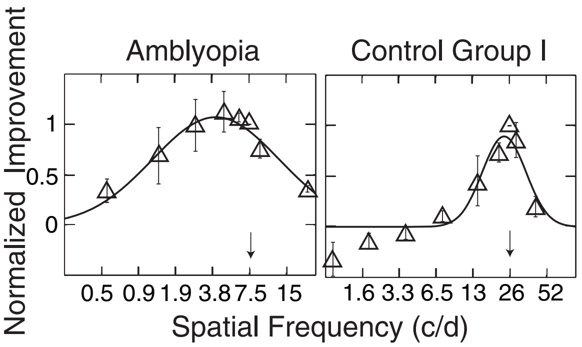

Fig. 5. Average contrast sensitivity improvements as a function of spatial frequency for the amblyopic group (*Left*) and first control group (*Right*). The magnitudes of contrast sensitivity improvements were normalized to that at the training spatial frequency; spatial frequencies were normalized to the training frequency. Arrows indicate the average training spatial frequency. Data were weighted by their standard deviation. Only observers with significant contrast sensitivity improvements during training are included. Error bars indicate SEM.

Various specificities have been used to distinguish perceptual learning from strategy change and other types of cognitive learning in normal adults. The broader generalization of perceptual learning in the amblyopic eyes seems to suggest that the performance improvements may reflect higher level learning or improved viewing strategy. We consider two possibilities:

(i) Learning at higher levels. This is unlikely because all of the subjects were college students and perfectly understood the task instructions before the experiment. They also participated in 700–900 instructional trials in each eye before data collection. In addition, performance improvements in the trained, amblyopic eyes are *greater* than those in the untrained, nonamblyopic eyes, indicating partial transfer between eyes. In another experiment (unpublished data), we found that perceptual learning at one orientation in the amblyopic eyes only *partially* generalized to the orthogonal orientation. Both forms of specificity suggest that perceptual learning in the amblyopic eyes is at a relatively low level of visual processing.

(ii) Improved accommodation and fixation. Again, this is an unlikely explanation. First, this study used briefly presented sinusoidal gratings, covering relatively large areas of the retina, which were robust to retinal motion. Second, Westheimer and McKee (34) showed that the spatial resolution of the visual system is immune to retinal image motion up to 2.5 °/s, which was faster than most fixational eye movements of amblyopes (35). Moreover, contrast sensitivity does not improve even when retinal image motion is eliminated by image stabilization (36).

Lu and Dosher (28, 37, 38) have argued that specificity of perceptual learning alone is an inadequate criterion for inferring the loci of perceptual learning. Instead, a systematic task analysis is necessary for the interpretation of various specificity tests and for the design of more diagnostic tests for the level of perceptual learning. This framework has revealed that the primary mechanisms of perceptual learning are the reduction of internal noise and

Table 1. Before training amblyopic observer characteristics

Subject	Sex	Age	Eye	Correction	Acuity (MAR), °	Training spatial frequency, c/°	No. training sessions
S1	F	16	AE	−4.00DS/−1.50DC × 180	3.0	10	10
			FE	−2.00DS	0.9		
S2	M	15	AE	+2.00DS	23.8	3	19
			FE	Plano	0.7		
S3	M	21	AE	+2.00DS	4.7	12	12
			FE	Plano	0.7		
S4	M	22	AE	+1.50DS	3.8	10	9
			FE	Plano	0.9		
S5	F	16	AE	+3.50DS	7.1	9.1	10
			FE	−1.00DS	1.2		
S6	F	17	AE	+7.00DS/+1.50 DC × 90	7.1	3	15
			FE	+1.25DS	0.7		
S7	F	21	AE	+7.50DS	6.0	4	12
			FE	Plano	0.6		
S8	F	22	AE	+6.00DS/+0.50 DC × 90	4.7	11	10
			FE	+1.50DS	0.9		
S9	F	20	AE	+2.75DS/+1.75 DC × 0	2.8	10	13
			FE	Plano	1.1		
S10	M	16	AE	+6.00DS/+1.00DC × 100	7.5	3	10
			FE	Plano	0.5		

MAR, minimum angle of resolution (°); AE, amblyopic eye; FE, fellow eye; DS, diopters sphere; DC diopters cylinder.

retuning of the perceptual template, reflecting reweighting of information from early sensory representations. Recent studies have reported that, compared with the normal visual system, the adult amblyopic visual system exhibits higher internal noise and deficient perceptual templates (39), even after a successful occlusion treatment (40). How do the current generalization results for amblyopic and normal vision relate to these results? How does learning at a high spatial frequency generalize to untrained frequencies and untrained eyes? We propose that the higher internal noise and defective perceptual templates in amblyopia may leave more room for improvements in perceptual learning. Specifically, if the dominant pretraining internal noise source in the amblyopic visual system is situated *after* the channels, then high-spatial frequency training that retunes frequency-specific templates while simultaneously reducing postchannel internal noise will manifest in the phenomenon of generalization across frequencies. Generalization across eyes would be observed if the internal noise source occurs after mixing of the channels in each eye. The question of generalization, and its proposed mechanism(s), needs further careful investigation.

In current clinical practice, adult amblyopia is mostly left untreated because it is widely believed that neural plasticity in the visual system diminishes with age after the critical period for spatial vision (usually before 6–8 years of age). Moreover, studies have shown that the classical "occlusion" treatment is no longer effective for older child and adult amblyopes (5). We suggest re-evaluating the conventional wisdom that passing the critical period results in a fully (although erroneously) developed visual system that is immune to therapeutic modifications. The current study, together with several others (5, 18–21), demonstrates that the adult amblyopic visual system remains remarkably plastic, and perceptual learning could lead to substantial improvements of spatial vision in adult amblyopia.

Materials and Methods

Observers. Ten teenage and adult observers (S1–S10; 18.6 ± 2.8 yr)[‡] with unilateral anisometropic amblyopia (see Table 1 for their characteristics) and 21 teenagers and adults with normal or corrected-to-normal vision participated in this study. Fourteen (S11–S24; 22.9 ± 1.7 yr) and seven (S25–S31; 22.6 ± 3.1 yr) normal observers were randomly assigned into the first and second control groups. Informed written consent was obtained.

Apparatus. All experiments were controlled by a PC running Psychophysics Toolbox (41). Stimuli were sinusoidal gratings displayed on a Sony G220 monitor with 640 × 480 pixel resolution, a frame rate of 85 Hz, and 27 cd/m^2 background luminance. Using a special circuit, the display system produced 14-bit gray-level resolution and was gamma-corrected (42). To minimize edge effects, a half-Gaussian ramp ($\sigma = 0.5°$) was used to blend the gratings into the background.

Observers placed their heads on a chin rest and viewed the displays monocularly. The display subtended 3.06° × 3.06° at a viewing distance of 2.28 m for observers in the amblyopic and second control group, and 1.53° × 1.53° at a viewing distance of 4.56 m for the first control group. The longer viewing distance was used to obtain gratings at high spatial frequencies.

Design. The experiment consisted of pretraining assessment, training, and post-training reassessment. In both pre- and post-training assessments, contrast sensitivity functions and visual acuity were measured in both eyes. Visual acuity was measured with the Chinese Tumbling E Chart and defined as the minimum angle of resolution (MAR) associated with 75% correct identification.

Contrast sensitivity was defined as the reciprocal of contrast threshold for detecting a grating with 79.3% accuracy. For the amblyopic and second control groups, contrast sensitivity was sampled at 0.5, 1, 2, 4, 8, 10, 12, 14, and 16 c/° in the trained eyes, and 0.5, 1, 2, 4, 8, 12, and 16 c/° in the untrained eyes. For the first control group, contrast sensitivity was sampled at 1, 2, 4, 8, 16, 24, and 32 c/°. A testing session of about 1 hr was needed to collect the contrast sensitivity function in each eye. All of the spatial frequencies were randomly mixed in each session. The order of CSF measurements was counterbalanced across observers.

In the training phase, observers practiced in a grating detection task near contrast threshold in the amblyopic eyes or the nondominant eyes. A staircase procedure was used to track the threshold contrast of the grating for each observer over the entire training course. A single spatial frequency was used for each observer. In the amblyopic and first control groups, observers were trained at their individual cut-off spatial frequencies (average, 7.5 ± 3.8 and 26.1 ± 4.2 c/°; median, 9.6 and 27 c/°), defined as the spatial frequency at which the contrast threshold was 0.50. Observers in the second control group were trained at 10 c/°, near the median cut-off spatial frequency of the amblyopes.

Each training session consisted of nine blocks of 120 trials each and lasted

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[‡] Data of seven of the amblyopes were included in the group average reported in ref. 20.

about 1 hr. Training was terminated after the observer achieved asymptotic performance for at least three consecutive sessions. The length of training ranged between 8 and 19 sessions [mean = 12 ± 3.1, 10.1 ± 0.9, and 10.9 ± 2.3 for the three groups, respectively; $F(2,28) = 2.19$, $P > 0.10$]. Subjects ran ≈700–900 practice trials in the CSF test in each eye before data collection.

Procedure. A two-interval forced-choice procedure was used for training and assessment of contrast sensitivity functions. Each trial started with a 259-ms fixation cross in the center of the display. This was followed by two 117-ms intervals, signaled by a brief tone in the beginning of each and separated by 500 ms. A grating was (randomly) presented in one of the two intervals. The other interval was blank. Observers indicated the signal interval by using the computer keyboard. During training, a brief tone followed each correct response; during contrast sensitivity function measurements, a brief tone followed each response regardless of its accuracy. The response also initiated the next trial.

Thresholds were measured with a three-down one-up staircase procedure in which three consecutive correct responses resulted in a reduction of signal contrast ($C_{n+1} = 0.90C_n$), and one wrong response resulted in an increase in contrast ($C_{n+1} = 1.10C_n$), converging to a performance level of 79.3% correct (43). One hundred trials were used to measure the contrast threshold at each spatial frequency. A reversal results when the staircase changes from increasing to decreasing contrast or vice versa. Following the standard practice, we averaged the contrasts of an even number of reversals to estimate the contrast threshold after excluding the first three or four reversals.

Data Analysis. Performance improvements at the training spatial frequency were assessed for each individual observer by performing a linear regression analysis on the learning curve: log contrast sensitivity as a function of log training session (44, 45). Contrast sensitivity functions were compared by using within-subject ANOVA. Improvement in visual acuity, VA_{imp}, was defined as the percentage change in the MAR:

$$VA_{\mathrm{imp}}\% = (1 - VA_{\text{post-training}}/VA_{\text{pre-training}}) \times 100\%. \quad [1]$$

Two different inclusion criteria were used in calculating the bandwidth of perceptual learning: (*i*) Only observers exhibiting improvements in the training phase (the slope of the learning curve is at least marginally different from zero, $P < 0.15$) were included in the analysis. Eight of the 10 observers in the amblyopic group and 9 of the 14 observers in the first control group satisfied the criterion. (*ii*) All of the observers were included. The resulting bandwidth estimates were statistically equivalent for both criteria ($P > 0.50$). The bandwidth estimates of those who did not show much performance improvement were unreliable and did not contribute much to the weighted average bandwidth.

The bandwidth of perceptual learning was estimated by using the following procedure: (*i*) The difference between the post- and pretraining contrast sensitivity functions for each observer was computed. (*ii*) For each observer, the magnitudes of contrast sensitivity improvements were normalized to that observed at the training spatial frequency; spatial frequencies were normalized to the training frequency. (*iii*) Normalized spatial frequencies [$\log_2(f/f_{\mathrm{training}})$] were then divided into nine bins: [−5, −4), [−4, −3), [−3, −2), [−2, −1), [−1, −0.5), [−0.5, 0), 0, (0, 0.5], and (0.5, 2]. Data within each bin were averaged, weighted by their standard deviations. (*iv*) The normalized contrast sensitivity improvements were fit with a Gaussian function:

$$\log[CS_{\text{post-training}}(f)] - \log[CS_{\text{pre-training}}(f)] = a\exp\left[-\left(\frac{\log_2(f) - \log_2(f_o)}{\sigma}\right)^2\right], \quad [2]$$

where a is the amplitude of the improvement, f is the normalized spatial frequency, f_o is the spatial frequency with the maximum improvement, and σ is the standard deviation of the Gaussian function. The bandwidth of perceptual learning was defined as

$$B = 2\sqrt{\ln 2}\,\sigma. \quad [3]$$

Two alternative methods were also used to estimate the average bandwidth of perceptual learning in each group: (*i*) Direct weighted fit of a single Gaussian function to the contrast sensitivity improvement function without binning. The method generated an equivalent solution to the binning method. (*ii*) An estimation of the bandwidth of perceptual learning of each observer followed by the computation of the weighted average bandwidth. The method generated slightly lower but not significantly different estimates of bandwidths for each group. Standard deviations of all of the estimated parameters were computed with a resampling method (46).

ACKNOWLEDGMENTS. We thank Drs. Liming Tao and Lixia Feng for recruiting and diagnosing the amblyopic subjects, and Zhuping Qiu and Fang Hou for participating in part of the experiments. This research was supported by Natural Science Foundation of China Grants 30128006 and 30630027, National Basic Research Program Grant 2006CB500804, and U.S. National Eye Institute Grant EY017491–05.

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