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Article

Perceptual Learning Improves Contrast Sensitivity of V1 Neurons in Cats

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Summary

Background: Perceptual learning has been documented in adult humans over a wide range of tasks. Although the often-observed specificity of learning is generally interpreted as evidence for training-induced plasticity in early cortical areas, physiological evidence for training-induced changes in early visual cortical areas is modest, despite reports of learning-induced changes of cortical activities in fMRI studies. To reveal the physiological bases of perceptual learning, we combined psychophysical measurements with extracellular single-unit recording under anesthetized preparations and examined the effects of training in grating orientation identification on both perceptual and neuronal contrast sensitivity functions of cats.

Results: We have found that training significantly improved perceptual contrast sensitivity of the cats to gratings with spatial frequencies near the "trained" spatial frequency, with stronger effects in the trained eye. Consistent with behavioral assessments, the mean contrast sensitivity of neurons recorded from V1 of the trained cats was significantly higher than that of neurons recorded from the untrained cats. Furthermore, in the trained cats, the contrast sensitivity of V1 neurons responding preferentially to stimuli presented via the trained eyes was significantly greater than that of neurons responding preferentially to stimuli presented via the "untrained" eyes. The effect was confined to the trained spatial frequencies. In both trained and untrained cats, the neuronal contrast sensitivity functions derived from the contrast sensitivity of the individual neurons were highly correlated with behaviorally determined perceptual contrast sensitivity functions.

Conclusions: We suggest that training-induced neuronal contrast gain in area V1 underlies behaviorally determined perceptual contrast sensitivity improvements.

Introduction

Perceptual learning has been documented over a wide range of perceptual tasks [1–4]. The observed specificity to the trained task or stimulus in perceptual learning has been generally interpreted as evidence for representation enhancement in early sensory cortical areas [2, 5, 6]. On the other hand, whereas cortical plasticity following extended practice has been documented in both auditory and somatosensory cortices [7, 8], evidence for such plasticity in early visual cortices is modest in neurophysiology, although some evidence has been reported in several fMRI studies [9–11].

Single-unit recording from monkey early visual areas [12–15] has demonstrated that perceptual learning is not clearly associated with increased neuronal recruitment or major changes of receptive field parameters in V1 and V2 [13, 14]. Schoups et al. [14] reported changes of the slopes of the neuronal orientation tuning curves, but the magnitude of the changes did not provide a compelling account of the large behavioral improvements. Ghose et al. [13] found no such changes in tuning curves in early visual areas, and only modest sharpening of tuning curves has been reported in V4 [15]. Other task-specific tuning changes observed in V1 [16], which may reflect selection of task-relevant stimulus features by attention, are incompatible with the representation enhancement hypothesis that predicts persistent and task-independent tuning changes. Law and Gold [17] found that perceptual learning in motion direction discrimination does not involve neuronal response changes in the middle temporal (MT) area, but rather in the lateral intraparietal area, a brain area related to selective readout of MT neurons. Finally, the related literature on cortical plasticity following lesions suggests that sensory cortical recruitment or remapping is nearly absent in V1 [18, 19]. In sum, these reports found that early visual representations showed either no change or modest changes in the slopes of tuning functions following perceptual learning.

In this study, we investigated the physiological bases of perceptual learning in adult cats. Cats have a highly developed visual system and have been widely used as an animal model in visual neuroscience [20, 21]. We have recently developed an effective training paradigm to compare perception and neural activity [22–24]. Existing neurophysiological investigations of cortical plasticity related to perceptual learning have primarily used nonprimate subjects in auditory and somatosensory studies and primate subjects in visual studies. It is possible that primates exhibit less training-induced plasticity than nonprimates in early visual areas [25, 26].

Previous neurophysiological studies on visual perceptual learning have predominantly used orientation discrimination tasks, which fix grating contrast and vary grating orientation to measure orientation thresholds (but see [17]). We trained cats to identify gratings at two fixed, widely separated grating orientations (±45°), and we varied grating contrast to measure contrast sensitivities [27–29]. Human subjects have demonstrated significant learning-induced improvements in contrast sensitivity functions that are specific to the trained spatial frequency and are partially specific to the trained eye, suggesting the primary visual cortex as the possible locus of learning [4, 30].

Conditioning was used to train two cats to identify the orientation of a high-contrast ±45° sinusoidal grating (Figure 1). Subsequently, the same procedure was used to measure

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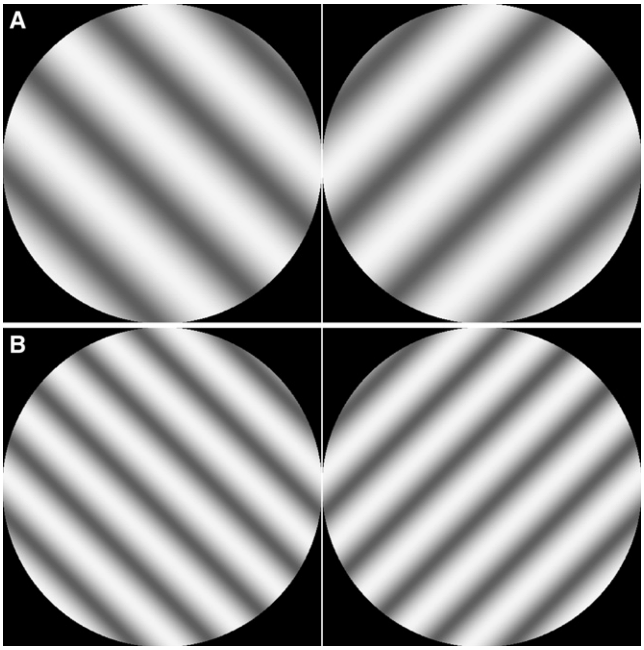

Figure 1. Visual Stimuli Used in Conditioning Training

(A) Visual stimuli for cat1, with spatial frequency of 0.2 cycle/degree (cpd). (B) Visual stimuli for cat2, with spatial frequency of 0.4 cpd. All stimuli are 80% contrast sine wave gratings oriented at ±45°.

monocular contrast sensitivity functions (CSFs) in both eyes. The cats were then trained monocularly to perform a near-contrast threshold orientation identification task (see Figure S1 available online). After approximately 40 days of training, monocular CSFs were measured again, followed by extracellular recordings of single-unit activities from the primary visual cortex (V1) of anesthetized cats. Contrast response functions to the preferred stimuli were measured for isolated neurons. The combined contrast sensitivities of individual neurons were then used to construct the neuronal CSFs for neuronal populations that responded preferentially to the stimuli presented via trained or untrained eyes.

We found that (1) training improved perceptual contrast sensitivity, with some degree of specificity for the training spatial frequency and training eye, (2) training also improved the contrast sensitivity of V1 neurons responding preferentially to the trained spatial frequency, (3) perceptual and neuronal CSFs were highly correlated both before and after training, and (4) training increased neuronal contrast gain.

Results

Perceptual Learning of Contrast Detection

Both cats completed conditioning training in 3–4 months. Prior to near-threshold training, the cats performed at 94% ± 4% correct on average (range: 90%–100%) in the high-contrast test across the full range of spatial frequencies. Their CSFs exhibited a significant main effect of spatial frequency (cat1: $F(6,84) = 105.11$; cat2: $F(6,84) = 142.35$; both $p < 0.0001$) but no significant effect of eye (cat1: $F(1,84) = 0.163$; cat2: $F(1,84) = 0.057$; both $p > 0.5$), nor frequency and eye interaction (cat1: $F(6,84) = 0.164$; cat2: $F(6,84) = 0.215$; both $p > 0.5$) (Figure 2).

Training significantly increased contrast sensitivity at the trained spatial frequency in the trained eye for both cats (Figure 3): sensitivity at the trained spatial frequency increased from 17.15 ± 2.83 (mean ± standard deviation) to 55.29 ± 7.38 for cat1 ($F(1,12) = 162.55$, $p < 0.0001$) and from 12.65 ± 3.43 to 39.76 ± 5.33 for cat2 ($F(1,12) = 128.01$, $p < 0.0001$). After training, the cats performed at 96% ± 4% correct level on average (range: 89%–100%) in the high-contrast tests, comparable to the pretraining performance levels ($p > 0.25$).

Training also significantly improved the CSFs in the trained eyes of both cats (cat1: $F(1,84) = 285.14$; cat2: $F(1,84) = 317.7$; both $p < 0.0001$). The magnitude of learning depended significantly on spatial frequency (cat1: $F(6,84) = 73.55$; cat2: $F(6,84) = 56.53$; both $p < 0.0001$) (Figures 2A and 2B): the ratio of post- versus pretraining sensitivity ranged from 1.15 to 3.31 with maximal improvement at 0.4 cycle/degree (cpd) for cat1 and from 1.06 to 3.37 with maximal improvement at 0.6 cpd for cat2. That the maximal sensitivity improvement was observed at the trained spatial frequency is indicative of spatial frequency specificity of perceptual learning [4, 30].

Perceptual learning in the trained eye also partially transferred to the untrained eye for both cats. Contrast sensitivity of the untrained eye at the trained spatial frequency improved from 16.53 ± 3.02 to 31.94 ± 3.81 for cat1 ($F(1,12) = 70.35$, $p < 0.0001$) and from 13.56 ± 2.94 to 27.81 ± 4.09 for cat2 ($F(1,12) = 55.9$, $p < 0.0001$), although the magnitude of improvement was significantly smaller than that in the trained eye for both cats (cat1: $F(1,12) = 55.18$, $p < 0.0001$; cat2: $F(1,12) = 22.13$; $p < 0.01$) (Figures 2A and 2B). In fact, partial transfer of perceptual learning happened in all spatial frequencies, i.e., the CSFs in the untrained eye improved following training (cat1: $F(1,84) = 80.98$; cat2: $F(1,84) = 112.16$; both $p < 0.0001$), with significant training and spatial frequency interactions (cat1: $F(6,84) = 23.77$; cat2: $F(6,84) = 21.19$; both $p < 0.0001$) (Figures 2A and 2B). The improvements occurred largely around the trained spatial frequency of each cat, around 0.2–0.6 cpd for cat1 and 0.4–0.8 cpd for cat2. The ratio of post- versus pretraining sensitivity ranged from 1.02 to 1.99 with maximal improvement at 0.4 cpd in cat1 and from 1.02 to 2.09 with maximal improvement at 0.6 cpd in cat2.

In summary, training greatly increased contrast sensitivity at the trained spatial frequency in the trained eye, with a certain degree of specificity for spatial frequency and the trained eye and significant partial transfer to untrained spatial frequencies and the untrained eye. Because the cats performed the task with high-contrast stimuli presented to either eye and across a wide range of spatial frequencies at a comparable level prior to and after training, the specificity results were not due to their inability to perform the task in different spatial frequencies or with untrained eyes before training.

Training-Induced Plasticity of V1 Neurons in Trained Cats

We systematically compared contrast sensitivities of V1 neurons of the trained and untrained cats, as well as neurons responding preferentially to stimuli presented via the trained and untrained eyes of the trained cats. A total of 142 and 117 cells in the trained and untrained cats were studied (Table 1). Cells recorded from each group of cats were at the same range of depth from the pial surface of the brain, representing random samples of neurons in all cortical layers. All cells had receptive fields within 8° of the area centralis. The eccentricity distribution of the receptive fields of cells recorded from V1 of trained cats was not significantly different from that of untrained cats ($x^2(15) = 10.725$, $p > 0.5$). Similarly, the eccentricity distributions of the receptive fields of cells

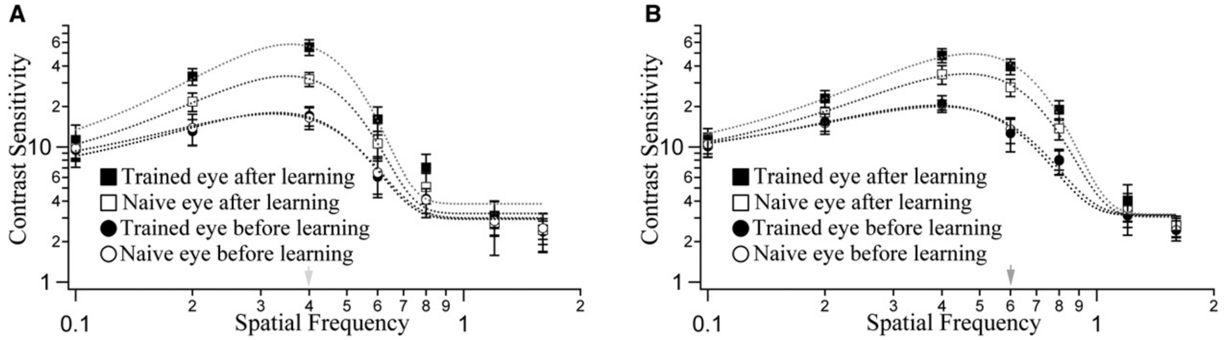

Figure 2. Contrast Sensitivity Functions in the Trained and Untrained Eyes before and after Training

(A) Cat1.

(B) Cat2.

Smooth curves represent the best-fitting Gaussian functions. The gray arrows indicate the trained spatial frequency, and the error bars represent 1 standard deviation (SD).

responding preferentially to stimuli presented via the trained and untrained eyes of the trained cats were not significantly different (cat1: $x^2(15) = 21.614$, $p > 0.10$; cat2: $x^2(15) = 22.857$, $p = 0.09$). In addition, the distributions of preferred spatial frequency and orientation were not significantly different between cells recorded from the trained and untrained cats ($x^2(34) = 45.41$, $p = 0.09$), cells responding preferentially to stimuli presented via the trained and untrained eyes of the trained cats ($x^2(30) = 23.560$, $p > 0.50$), and cells responding preferentially to stimuli presented via the trained eyes of the trained cats and cells from the untrained cats ($x^2(33) = 40.17$, $p > 0.15$).

Comparison between Trained and Untrained Cats

We first compared the contrast sensitivities of neurons from the trained and untrained cats. Neurons were grouped by their preferred spatial frequencies. We ignored their preferred orientations, temporal frequencies, and motion directions because perceptual learning in contrast detection is largely nonspecific in those dimensions [4, 13, 31]. Additional analysis on the response characteristics of the neurons with preferred orientation near and away from the trained orientations was also performed. For each neuron, two measures of contrast sensitivity were computed from its contrast response function (Figure 4). Threshold stimulus contrast (TC) sensitivity is the inverse of each neuron's threshold contrast, which evokes 1.414× its spontaneous activity. C_{50} contrast sensitivity is defined as the inverse of C_{50}, which evokes half of a cell's maximal response (Figures S2 and S3). Comparisons were made between cells from each trained cat and all of the untrained cats.

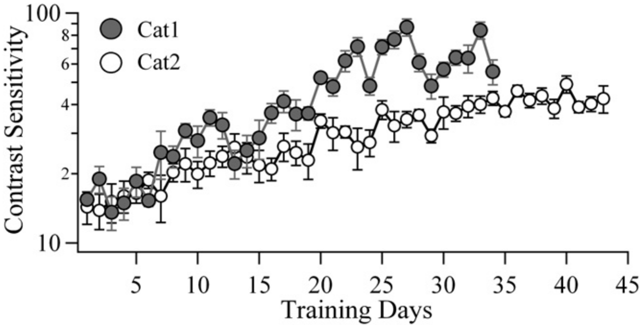

Figure 3. Contrast Sensitivity at the Trained Spatial Frequency versus Training Days

Cat1: filled circles. Cat2: open circles. The error bars represent 1 SD.

The mean TC contrast sensitivity of neurons recorded from the trained cats was significantly higher than that of cells from the untrained cats (cat1: $F(1,196) = 6.181$, $p < 0.05$; cat2: $F(1,152) = 15.374$, $p < 0.0001$), with strong dependence on spatial frequency (cat1: $F(6,196) = 4.056$, $p < 0.001$; cat2: $F(6,152) = 9.591$, $p < 0.0001$) (Figures 5A and 5B; Table 1). Similarly, the mean C_{50} contrast sensitivity of neurons recorded from the trained cats was also significantly increased compared with that of cells from the untrained cats (cat1: $F(1,196) = 13.131$, $p < 0.0001$; cat2: $F(1,152) = 14.873$, $p < 0.0001$), also with strong dependence on spatial frequency (cat1: $F(6,196) = 5.171$, $p < 0.0001$; cat2: $F(6,152) = 5.901$, $p < 0.0001$) (Figures 5C and 5D; Table 1; Figure S3).

Eye and Spatial Frequency Specificity of Training-Induced Plasticity of V1 Neurons

For both trained cats, significant differences were found between the mean contrast sensitivity of neurons responding preferentially to stimuli presented via the trained and untrained eyes of the trained cats at their respective training spatial frequencies: 0.4 cpd for cat1 (TC: $F(1,26) = 5.32$, $p < 0.03$; C_{50}: $F(1,26) = 6.744$, $p < 0.02$) and 0.6 cpd for cat2 (TC: $F(1,10) = 24.61$, $p < 0.001$; C_{50}: $F(1,10) = 15.03$, $p < 0.003$), although nonsignificant or marginal difference was found between the mean neuronal contrast sensitivities if neurons responding to the full range of spatial frequencies were included (cat1: TC: $F(1,79) = 1.118$, $p > 0.25$, C_{50}: $F(1,79) = 1.800$, $p > 0.15$; cat2: TC: $F(1,35) = 4.042$, $p = 0.05$, C_{50}: $F(1,35) = 2.94$, $p = 0.09$) (Figures 5A–5D; Table 1; Figure S3). We conclude that training-induced plasticity of V1 neurons exhibited a degree of specificity to the trained eye and trained spatial frequency, consistent with our psychophysical results.

Comparing Perceptual and Neuronal CSFs

We constructed neuronal CSFs by averaging contrast sensitivities of all of the neurons with the same preferred spatial frequencies (Figure 6). For the trained eyes, the pretraining perceptual CSFs of cat1 and cat2 were significantly correlated with the average neuronal CSFs of the three untrained cats with either TC (cat1: $r = 0.960$; cat2: $r = 0.951$; both $p < 0.001$)

Table 1. Contrast Sensitivity of V1 Neurons

			Spatial Frequency (Cycle/Degree)						
Subjects	Eye	n/CS	0.1	0.2	0.4	0.6	0.8	1.2	1.6
Control cats	Both	n	15	28	32	18	8	9	7
		TCS	8.6 ± 1.3	11.2 ± 1.6	16.4 ± 2.3	8.8 ± 1.8	4.5 ± 0.7	4.1 ± 0.7	4.9 ± 1.3
		C_{50}CS	2.9 ± 0.4	4.1 ± 0.6	5.1 ± 0.6	3.0 ± 0.3	2.6 ± 0.3	1.9 ± 0.2	1.8 ± 0.3
Trained cat1	Trained	n	9	13	15	6	3	3	2
		TCS	8.8 ± 2.1	26.4 ± 6.7	50.3 ± 6.7	13.6 ± 2.2	6.4 ± 0.9	4.7 ± 1.0	4.2 ± 1.1
		C_{50}CS	3.8 ± 0.3	6.0 ± 0.4	13.3 ± 1.2	5.4 ± 0.6	2.7 ± 0.3	2.9 ± 0.6	2.6 ± 0.8
	Naive	n	4	7	13	7	6	3	2
		TCS	7.3 ± 2.6	20.3 ± 3.8	27.5 ± 7.2	11.1 ± 2.5	5.3 ± 0.7	4.2 ± 2.0	4.3 ± 2.1
		C_{50}CS	3.3 ± 0.9	4.8 ± 0.6	8.6 ± 1.4	4.6 ± 0.8	3.1 ± 0.5	2.5 ± 1.1	2.6 ± 1.1
Trained cat2	Trained	n	2	3	9	7	3	2	2
		TCS	8.7 ± 1.6	10.0 ± 1.5	47.7 ± 3.9	34.1 ± 1.8	11.9 ± 2.0	2.9 ± 0.5	2.7 ± 0.2
		C_{50}CS	2.8 ± 0.3	4.4 ± 1.3	11.4 ± 1.2	11.3 ± 1.0	4.6 ± 0.5	1.6 ± 0.1	1.5 ± 0.2
	Naive	n	2	3	5	5	2	2	2
		TCS	9.1 ± 0.8	10.4 ± 2.2	31.8 ± 3.2	18.6 ± 2.7	8.1 ± 0.2	3.8 ± 1.2	3.8 ± 1.5
		C_{50}CS	3.0 ± 0.6	4.1 ± 0.6	7.8 ± 1.0	6.5 ± 0.6	4.7 ± 1.3	1.9 ± 0.3	1.7 ± 0.2

The following abbreviations are used: CS, contrast sensitivity; n, number of cells; TCS and C_{50}CS, TC contrast sensitivity (1/TC) and C_{50} contrast sensitivity (1/ C_{50}), respectively. Their values are expressed as mean ± SEM.

or C_{50} contrast sensitivity (cat1: $r = 0.970$; cat2: $r = 0.981$; both $p < 0.0001$) as the index of neuronal contrast sensitivities. After training, the posttraining perceptual CSFs of the trained cats were also significantly correlated with the neuronal CSFs of neurons responding preferentially to stimuli presented via the trained eyes, based on both TC (cat1: $r = 0.994$; cat2: $r = 0.963$; both $p < 0.001$) and C_{50} contrast sensitivity measures (cat1: $r = 0.962$, $p < 0.001$; cat2: $r = 0.977$, $p < 0.0001$). Moreover, the observed magnitude of improvements of the perceptual CSF of the trained eye was also highly correlated with changes of the neuronal CSFs of neurons responding preferentially to stimuli presented via the trained eye of each trained cat relative to the three untrained cats, based on TC (cat1: $r = 0.906$, $p < 0.01$; cat2: $r = 0.971$, $p < 0.0001$) and C_{50} contrast sensitivity (cat1: $r = 0.700$, $p < 0.05$; cat2: $r = 0.967$, $p < 0.0001$).

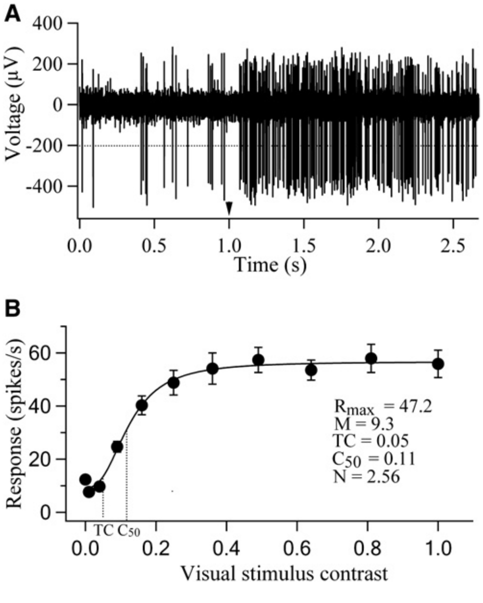

Figure 4. A Typical Neuron's Response to Its Optimal Visual Stimulus

(A) The voltage trace of the neuron's response to the optimal stimulus at 64% contrast. A spike with amplitude surpassing the horizontal broken line is counted as an action potential. The neuron's response is evoked by 5 cycles of grating stimulation, equivalent to a stimulus duration of about 1.7 s, and the spontaneous activity (M) is acquired 1 s prior to visual stimulus presentation. The arrowhead indicates the stimulus onset time.

(B) Contrast response function of the neuron (mean ± SD). The smooth curve represents the best-fitting Naka-Rushton equation ($r^2 = 99.5\%$). M and R_{max} represent the neuron's spontaneous activity and maximal visually evoked response to visual stimuli. Threshold stimulus contrast (TC) represents the stimulus contrast that evokes a neuron's response that is 1.414× its spontaneous activity. C_{50} corresponds to the stimulus contrast that evokes half of the neuron's maximal response. N represents the slope of the neuron's response-contrast tuning curve.

In the untrained eyes, the pretraining perceptual CSFs of cat1 and cat2 were significantly correlated with the average neuronal CSFs of the three untrained cats with either TC (cat1: $r = 0.952$, $p < 0.0001$; cat2, $r = 0.945$; both $p < 0.01$) or C_{50} contrast sensitivity (cat1: $r = 0.964$; cat2: $r = 0.965$; both $p < 0.0001$) as the index of neuronal contrast sensitivity. After training, the posttraining perceptual CSFs in cat1 and cat2 were also significantly correlated with the neuronal CSFs of neurons responding preferentially to stimuli presented via the corresponding untrained eyes based on both TC (cat1: $r = 0.992$; cat2: $r = 0.951$; both $p < 0.0001$) and C_{50} contrast sensitivity measures (cat1: $r = 0.95$, $p < 0.001$; cat2: $r = 0.983$, $p < 0.0001$). Further, the observed magnitude of CSF improvements of the untrained eye were also highly correlated with changes of the neuronal CSFs of neurons responding preferentially to stimuli presented via the untrained eye of each trained cat relative to three untrained cats based on TC contrast sensitivity (cat1: $r = 0.827$, $p < 0.05$; cat2: $r = 0.947$, $p < 0.01$).

Mechanisms of Contrast Sensitivity Enhancement of V1 Neurons

Four potential mechanisms may underlie the training-induced contrast sensitivity improvements [32–36]: (1) decreased spontaneous activities (M), (2) increased responsiveness (R_{max}), (3) increased slopes of contrast response functions (N), and (4) increased contrast gain (C_{50}). We systematically compared the best-fitting parameters of the Naka-Rushton equation in different neuronal populations (Figure 4B; Figure S2).

No significant difference was found between the trained and untrained cats in terms of spontaneous activities ($F(1,254) = 1.946$, $p > 0.1$), maximum responses ($F(1,254) = 0.05$, $p > 0.5$), or slopes of contrast response functions ($F(1,254) = 3.319$, $p = 0.07$), nor was there significant difference between neurons responding preferentially to stimuli presented via

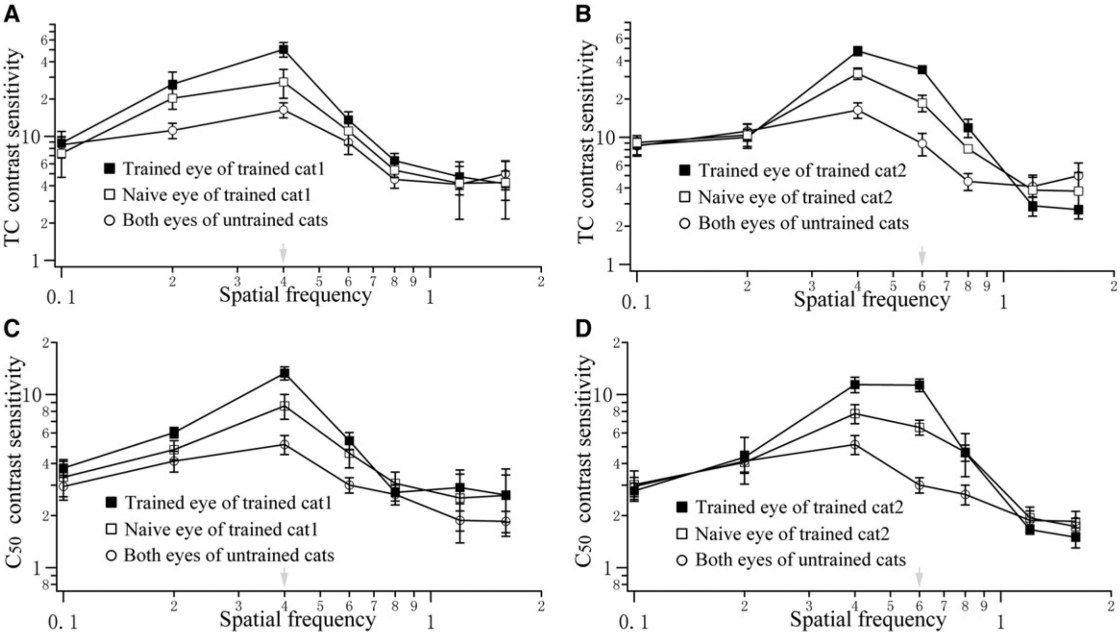

Figure 5. Neuronal Contrast Sensitivity Functions

(A and B) TC contrast sensitivity functions of V1 neurons recorded from cat1 (A) and cat2 (B).

(C and D) C_{50} contrast sensitivity functions of V1 neurons recorded from cat1 (C) and cat2 (D). The arrows indicate the trained spatial frequency. All values are displayed as mean ± standard error of the mean (SEM).

the trained and untrained eyes of the trained cats in spontaneous activities (cat1: $F(1,91) = 0.093$, $p > 0.50$; cat2: $F(1,47) = 0.141$, $p > 0.50$), maximum responses (cat1: $F(1,91) = 3.196$, $p = 0.08$; cat2: $F(1,47) = 1.333$, $p > 0.25$), or the slopes of contrast response functions (cat1: $F(1,91) = 2.691$, $p > 0.1$; cat2: $F(1,47) = 3.232$, $p = 0.08$) (Figures 7A–7C). In contrast, there was a significant difference between the trained and untrained cats in terms of C_{50} ($F(1,254) = 37.487$, $p < 0.0001$) (Figure 7D) and between neurons responding preferentially to stimuli presented via the trained and untrained eyes of the trained cats around their respective training spatial frequency (Figures 7E and 7F), 0.2–0.6 cpd for cat1 ($F(1,59) = 8.855$, $p < 0.01$) and 0.4–0.8 cpd for cat2 ($F(1,29) = 9.774$, $p < 0.01$).

We also compared posttraining maximal response, TC contrast sensitivity, and C_{50} contrast sensitivity between neurons with preferred orientation near (within ±15°) and away from the trained orientations in two trained cats. We found no significant difference (maximal response: $F(1,140) = 0.211$, $p = 0.647$; TC contrast sensitivity: $F(1,140) = 0.134$, $p = 0.715$; C_{50} contrast sensitivity: $F(1,140) = 0.0001$, $p = 0.995$). We also compared posttraining maximal response, TC contrast sensitivity, and C_{50} contrast sensitivity of neurons with preferred orientation near the trained orientations between the trained and untrained cats. The mean maximal response of neurons with preferred orientation near the trained orientations in trained cats was not significantly different from that in

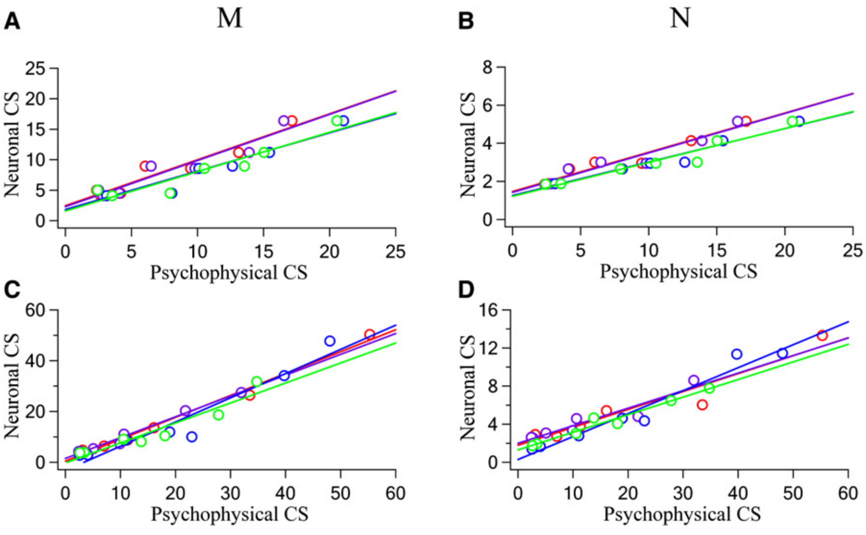

Figure 6. Scatter Plots of Neuronal Contrast Sensitivity versus Psychophysical Contrast Sensitivity

Colored circles represent, respectively, the trained and untrained eyes of the trained cats (red circle: trained eye of trained cat1; purple circle: untrained eye of trained cat1; blue circle: trained eye of trained cat2; green circle: untrained eye of trained cat2). Neuronal contrast sensitivity is based on TC in (M) and based on C_{50} in (N).

(A and B) Contrast sensitivities before training.

(C and D) Contrast sensitivities after training. Colored lines in each subplot represent the best linear fits (red: trained eye of trained cat1; purple: untrained eye of trained cat1; blue: trained eye of trained cat2; green: untrained eye of trained cat2.).

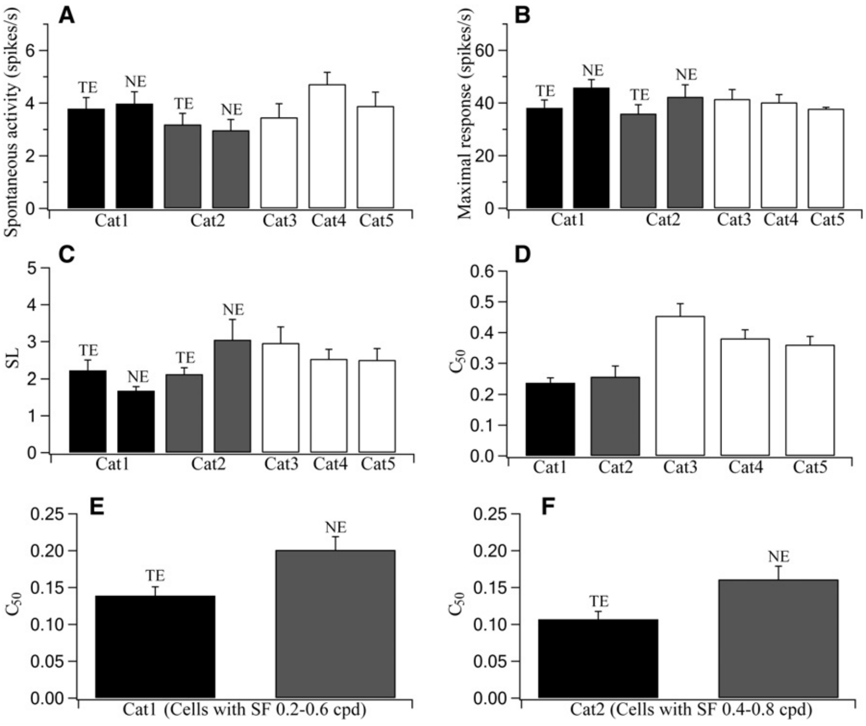

Figure 7. Parameters of the Best-Fitting Naka-Rushton Equation to the Neuronal Contrast Response Functions

(A) Spontaneous activities.

(B) Maximum responses.

(C) Slopes of the contrast response functions (SL).

(D) Contrast gain (C_{50}) of cells in each trained and control cat.

(E) Contrast gain of cells with optimal spatial frequency of 0.2–0.6 cpd in trained cat1.

(F) Contrast gain of cells with optimal spatial frequency of 0.4–0.8 cpd in trained cat2. TE and NE denote cells responding preferentially to the stimuli presented via the trained eye and the naive eye. All values are expressed as mean ± SEM.

untrained cats (F(1,39) = 0.247, p = 0.622). However, the mean TC contrast sensitivity (F(1,39) = 4.589, p = 0.038) and C_{50} contrast sensitivity (F(1,39) = 7.189, p = 0.011) showed a significant difference between the trained cats and untrained cats.

We conclude that the improved contrast sensitivity in the trained eyes of the trained cats can be attributed to increased contrast gain of neurons responding preferentially to stimuli presented via the trained eyes, corresponding to a leftward shift of the neuronal contrast response functions [32, 34, 35] and consistent with the stimulus enhancement mechanism in human behavioral studies [36].

Discussion

In this study, we examined the physiological bases of perceptual learning by combining psychophysical assessment of contrast sensitivity and extracellular single-unit recording on cats. We found that training significantly improved the contrast sensitivity of the cats to gratings with spatial frequencies near the trained spatial frequency. The learning effect also exhibited specificity to the trained eye, although there was partial transfer to the untrained eye. Consistent with the psychophysical observations, the mean contrast sensitivity of V1 neurons with preferred spatial frequency near the trained spatial frequency was significantly increased in the trained cats relative to the untrained cats; specifically, the mean contrast sensitivity of neurons responding preferentially to stimuli presented via the trained eyes of the trained cats was significantly higher than the untrained eyes of the trained cats. Moreover, the perceptual and neuronal CSFs in the trained and untrained cats, and the trained and untrained eyes of the trained cats, showed a remarkable degree of correlation prior to and after training. The magnitude of neuronal contrast sensitivity improvements is also highly correlated with that of performance improvements at the whole animal level. These results suggest that training in grating orientation identification leads to improvements of contrast sensitivity of V1 neurons and, therefore, improved perceptual contrast sensitivity. We further determined that increased contrast gain underlay improved neuronal contrast sensitivities.

The results of our study are different from other visual physiological studies on visual perceptual learning. There are three critical differences between our study and those in the literature:

1. Different species: Whereas neurophysiological studies of visual perceptual learning in the literature all used primate subjects, the current study used nonprimates (cats). This difference may be very important, because significant training-induced plasticity has been widely reported in auditory and somatosensory cortices of nonprimates [7, 8], and it has been shown that a short-term (a few hours) intracortical microstimulation could lead to drastic changes of orientation preference maps in the visual cortex of adult cats [37].
2. Different tasks: As shown by some fMRI studies, training-induced neural plasticity may depend considerably on visual tasks [9–11]. Previous electrophysiological studies exploring training-induced visual cortical plasticity generally used orientation threshold as the dependent measure. However, the current study used contrast threshold as the dependent measure and yielded a result quite different from others, suggesting that different neural networks might be involved in orientation discrimination and contrast detection.
3. Different animal states: We recorded the response of V1 neurons in anesthetized and paralyzed cats, whereas previous studies made recordings in awake-behaving monkeys. Compared to studies on anesthetized cats, recordings from early visual cortical areas of awake monkeys may include substantial top-down influences from higher visual cortical areas [16, 38, 39].

We are conducting new studies to further investigate all of these factors.

That contrast sensitivity of visual perception in the trained cats improved significantly near the trained spatial frequency is consistent with previous observations in human studies [1, 4, 40]. Similar results were also obtained in our physiology recordings, suggesting that perceptual learning in contrast detection is likely mediated through spatial frequency channels in the primary visual cortex in cats. Mixed results on eye specificity of visual perceptual learning have been reported in the literature [2, 4, 5, 23, 41]. In this study, we found that perceptual learning of contrast detection transferred partially to the untrained eye, with a certain degree of eye specificity. The results suggest that the training-induced plasticity may occur both before and after binocular combination. Subsequent experiments are needed to examine the learning effects that may have likely occurred in the dorsal lateral geniculate nucleus (dLGN). For example, one can examine the differences in training-induced plasticity between x and y channels by presenting low spatial frequency stimuli to the animal and recording single neuron activity from area 18 (V2), which receives substantial direct y channel (but not x channel) input from the dLGN. Another way is to examine whether training can modify the suppressive surround receptive fields of V1 and V2 neurons, with preferred spatial frequency near the trained spatial frequency.

Our neurophysiological data showed that perceptual learning in contrast detection led to enhanced contrast sensitivities of V1 neurons with preferred spatial frequency near the trained spatial frequency. A systematic analysis of the parameters of the neuronal contrast response functions indicated that this training-induced plasticity was caused by increased contrast gain of the neurons associated with training, not by lowered spontaneous activity, increased responsiveness of V1 neurons, or increased slopes of neuronal contrast response functions. The increased contrast gain resulted in a parallel leftward shift of the neuronal contrast response functions, consistent with decreased postsynaptic polarization [42, 43], but not changes in presynaptic processes [44, 45], which would have resulted in changes of the maximum response level and slope of contrast response functions. Future experiments with in vivo patch-clamp recordings are necessary to further elucidate the underlying cellular mechanisms of perceptual learning.

We conclude that training in grating orientation identification increased contrast gain of neurons that respond preferentially to stimuli presented via the trained eye and with spatial frequency near the trained spatial frequency. The neuronal changes led to behavioral contrast sensitivity improvement of cats, with a certain degree of specificity to the trained spatial frequency and trained eye.

Experimental Procedures

Subjects

Five adult male cats (age: 1–3 yrs old; body weight: 2.2–3 kg) with no apparent optical or retinal problems served as subjects. Cat1 and cat2 received training; the other three cats were control subjects. Animal treatments were strictly in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals.

Psychophysical Procedures

The training apparatus was similar to that used in the literature [24, 46]. At first, cat1 and cat2 received monocular conditioning training in a two-alternative forced-choice grating orientation identification task with fixed, high-contrast (80%) grating stimuli at a single spatial frequency and which were oriented ±45°. The spatial frequency was set at 0.2 cpd for cat1 and 0.4 cpd for cat2 (Figures 1A and 1B). The mean luminance of grating stimuli was kept at 19 cd/m^2. The untrained eye was covered with a special mask that blocked light.

The experimenter triggered the first trial in the beginning of each training block when everything was ready. Each trial started with a bright fixation dot (0.1° visual angle) that appeared in the center of the cathode ray tube for 1 s. This was followed by a 4 s stimulus presentation with a 1 s response-denied period, during which pushing the nose keys triggered no food reward. Because large-size sine wave gratings were used in the study, eye fixation was not important and was not monitored. A 4 s interstimulus interval was provided between trials.

Cat1 and cat2 concluded their conditioning training after >90% mean correct performance was attained in six consecutive days. This was then followed by measurement of pretraining CSFs in the trained and untrained eyes, monocular training of near-contrast threshold grating identification at a single spatial frequency for 40 days, measurement of posttraining CSFs, and tests of their performance via high-contrast sine wave gratings. The same grating orientation identification task was used, except contrast thresholds were measured. Contrast thresholds at 0.1, 0.2, 0.4, 0.6, 0.8, 1.2, and 1.6 cpd (560 trials of test for each spatial frequency, all intermixed) were measured to construct seven repeated measures of CSFs, one from each of 80 trials per spatial frequency. Gratings at 0.4 cpd and 0.6 cpd were used to train cat1 and cat2, respectively.

A two-down/one-up staircase procedure was used to measure contrast thresholds (Figure S1). Contrast sensitivity at each spatial frequency was defined as the log of the reciprocal of mean threshold contrast. The contrast sensitivity functions were fit with the Gaussian equation

$$CSF(f) = CSF_0 + A\exp\left[-\frac{(f-f_0)^2}{width^2}\right],$$

where f is the spatial frequency of the grating, f_0 is the peak spatial frequency, and A is the maximum sensitivity. The CSFs prior to and after learning were compared via analysis of variance based on repeated measurements.

In each daily training session, the subject was administered 1000–1500 trials in 10–15 blocks of 100 trials. Subjects took 5–10 min breaks between blocks.

Electrophysiological Recording

Following the psychophysical experiment, all five cat subjects were prepared for extracellular single-unit recording via procedures described in previous publications [22] (Supplemental Experimental Procedures). The response of a cell to a drifting sinusoidal grating was defined as the mean response value (after subtracting the baseline) corresponding to the time of stimulus modulation, which was used to draw the spatial frequency, orientation, and contrast tuning curve (Figures 4A and 4B).

The contrast response function of each neuron was fit with the Naka-Rushton equation [47]

$$R(C) = R_{max}\frac{C^N}{\left(C^N + C_{50}^N\right)} + M,$$

where R_{max} is the maximal response, M is the spontaneous activity, C_{50} is the contrast that evokes half of the maximal response, and N represents the slope of the contrast response function. Cells with less than 95% goodness of fit were not included in our data analysis. 7.2% of cells were excluded.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at doi:10.1016/j.cub.2010.03.066.

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