



# The effect of orientation learning on contrast sensitivity

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## Abstract

Regan and Beverley [Regan, D., & Beverley, K. I. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America A*, 2(2), 147–155] previously demonstrated that adapting to an oriented visual stimulus improves sensitivity to subtle orientation differences while impairing contrast sensitivity. Here, we investigated whether practice-based improvements in orientation sensitivity would, like adaptation, impair contrast sensitivity. To the contrary, we found that contrast sensitivity actually improved significantly after observers demonstrated practice-based increases in orientation sensitivity. Therefore, while orientation sensitivity can be enhanced either by orientation-discrimination training or by adapting to visual stimuli, these two procedures have opposite effects on contrast sensitivity. This difference suggests that adaptation and perceptual learning on orientation discrimination cannot be explained sufficiently by a shared underlying cause, such as a reduction in neural activity. © 2001 Elsevier Science Ltd. All rights reserved.

**Keywords:** Perceptual learning; Orientation discrimination; Contrast sensitivity; Adaptation

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## 1. Introduction

It is well established that, with practice, adult humans can become more sensitive to subtle orientation differences between two visual stimuli (Vogels & Orban, 1985; Schoups, Vogels, & Orban, 1995; Chen & Levi, 1996; Matthews & Welch, 1997; Matthews, Liu, Geesaman, & Qian, 1999; Rivest, Boutet, & Intriligator, 1997; Doshier & Lu, 1999). The physiological changes that underlie these practice-based improvements in orientation sensitivity have been the focus of several recent experiments. For example, a recent study using positron emission tomography indicated that after human observers demonstrated learning on orientation discrimination, blood flow in the striate and extrastriate visual cortex was significantly reduced (Schultz, Bodart, Dubois, Dejardin, Michel, Roucoux, Crommelinck, & Orban, 1999). Correspondingly, preliminary electrophysiological data from monkey striate cortex suggest that after orientation-discrimination training, neurons tuned to the trained orientation exhibit firing-rate re-

ductions (Ghose & Maunsell, 1997; Schoups, Vogels, & Orban, 1998).

One account of how reductions in neural activity might improve orientation sensitivity was offered by Regan and Beverley (1985). They had observers continuously view an oriented stimulus and found that, near the adapting orientation, contrast sensitivity decreased while orientation sensitivity increased transiently. Their explanation for these opposing effects is shown schematically in Fig. 1, which posits three hypothetical neural elements (A–C) with different orientation preferences. Before adaptation (top panel), element B would be more effective than either element A or C for detecting a low-contrast stimulus presented at orientation B. Note, however, that element B would give identical responses to stimuli presented slightly anti-clockwise or clockwise to its preferred orientation (dotted vertical lines). Therefore, element B would contribute nothing, or perhaps noise, to judgments about subtle angular changes occurring around its preferred orientation. Of course, these subtle angular changes could be identified by comparing the relative responses of elements A and C, provided that such a comparison were not ‘swamped’ by noise from element

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B. After observers continually view a stimulus at orientation B, the maximal response from element B is reduced to B' (bottom panel). Consequently, contrast sensitivity to orientation B has decreased. Yet, subtle angular changes near orientation B can now more easily be identified by comparing responses from elements A and C, since noise from element B has been reduced. Thus, the reduction in firing that presumably follows from adaptation can impair contrast sensitivity while improving orientation sensitivity.

The decreases in the firing rate of element B could also improve orientation discrimination for another reason. Within the framework of a recurrent network model (Somers, Nelson, & Sur, 1995; Carandini & Ringach, 1997), it has been shown computationally that firing-rate reductions at the trained orientation can sharpen the tuning of cells near the trained orientation, and broaden the tuning of cells preferring orientations somewhat further away (Qian & Matthews, 1999). This selective sharpening and broadening of orientation–tuning curves is sufficient to improve orientation discrimination.

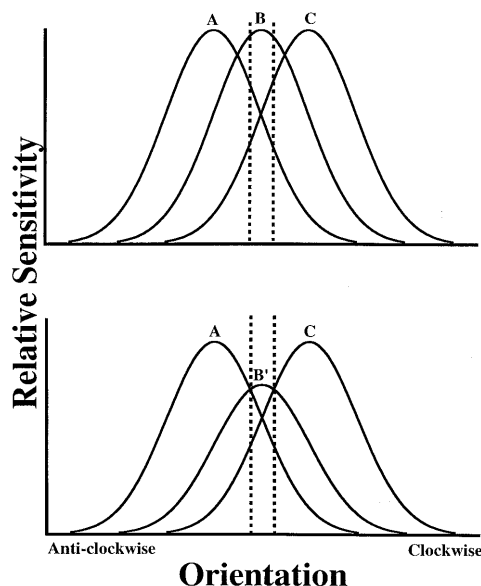


Fig. 1. Hypothetical orientation-selective neural elements (adapted from Regan & Beverley, 1985). Before observers have adapted (top panel), element B is the most effective of the three elements for detecting faint stimuli near its preferred orientation. However, element B contributes either nothing or noise to the discrimination of subtle orientation differences (dotted vertical lines) around its preferred orientation. These orientation differences could be detected by comparing responses from elements A and C, unless the comparison is rendered unreliable by noise from element B. (bottom panel). The response from all three elements is reduced after prolonged viewing of a stimulus at orientation B, but the reduction is most pronounced for element B (compare B to B'). This reduction impairs contrast sensitivity to faint stimuli presented near orientation B. However, orientation differences can now be more readily identified by comparing responses from elements A and C, because noise from element B has been reduced. Thus, adaptation enhances orientation sensitivity while impairing contrast sensitivity.

Given these considerations and the physiological data from the perceptual learning studies (Ghose & Maunsell, 1997; Schoups et al., 1998; Schiltz et al., 1999), it may be hypothesized that adaptation and perceptual learning on orientation discrimination can be explained by a shared underlying cause — a reduction in neural activity<sup>1</sup>. A prediction from this hypothesis is that practice-based improvements in orientation sensitivity should, like adaptation, be associated with a reduction in contrast sensitivity. Accordingly, we measured contrast sensitivity before and after observers trained on orientation discrimination. Contrary to the hypothesis, we found that contrast sensitivity did not decrease, but actually increased significantly after orientation learning. We believe this result implies that although improvements in orientation sensitivity can be generated by either an adaptation paradigm (Regan & Beverley, 1985) or a perceptual learning paradigm, the phenomena of adaptation and perceptual learning cannot be explained sufficiently by a shared underlying cause.

## 2. Methods

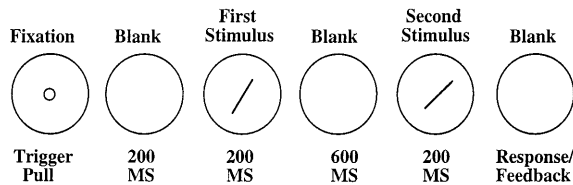
### 2.1. Apparatus and stimuli

Both the orientation-discrimination task and the contrast-detection task were conducted on a 21 in. (53.34 cm) ViewSonic Professional Series PT180 monitor. The monitor was controlled by a Macintosh-compatible PowerTower Pro 225 computer and a psychophysics software package developed in our laboratory (Geesaman & Qian, 1996). The vertical refresh rate of the monitor was set to 100 Hz, and the spatial resolution was set to 1024 pixels by 764 pixels. Stimuli were single lines, each 2° long, 5 arcmin wide, and presented for just 200 ms to minimize eye movements. Also, a circular fixation point with a diameter subtending 12 arcmin was presented on each trial. To eliminate unwanted screen persistence the luminance of the line stimulus was always less than the veiling luminance of 47 cd/m<sup>2</sup>. A chin rest helped to stabilize the viewing distance of 57 cm. All responses were made via a Sidewinder 3D Pro joystick (Microsoft Inc.), and both tasks were conducted in a well-lit room.

On the orientation-discrimination task, stimuli were viewed through a black, circular tube having an inner diameter of 10 cm. The circular viewing tube extended

<sup>1</sup> That the activity reduction is long-lasting for learning and transient for adaptation could explain the fact that the improvement in orientation sensitivity is long-lasting after learning and transient after adaptation (but see McCollough, 1965 for an enduring adaptation effect). While the precise neural locus of the activity reduction is not critical to our hypothesis, activity reductions induced by adaptation paradigms (Vautin & Berkley, 1977; Movshon & Lennie, 1979; Sclar et al., 1989) and perceptual-learning paradigms (Ghose & Maunsell, 1997; Schoups et al., 1998; Schiltz et al., 1999) have been observed in the primary visual cortex.

## Orientation-Discrimination Trial



## Contrast-Detection Trial

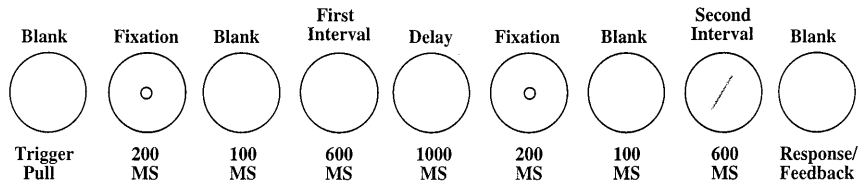


Fig. 2. Trial sequence. The sequence of events is shown for the orientation-discrimination task (top) and the contrast-detection task (bottom). Each task began when the observer pulled the trigger on a Joystick, and ended with auditory feedback indicating a correct or incorrect response. On the orientation-discrimination task, observers judged whether the second stimulus was tilted clockwise or anti-clockwise to the first. In the example shown here, the correct response is 'clockwise'. On the contrast-detection task, observers reported whether the stimulus was shown in the first interval or the second interval. In the example shown here, the correct response is 'second interval'.

from the observers' eyes to the computer screen, thereby preventing observers from using external references to determine the orientation of the stimuli. Given previously reported thresholds for oblique orientation-discrimination (Vogels & Orban, 1985; Heeley & Timney, 1988; Matthews & Welch, 1997; Orban & Vogels, 1998), the orientation of the two stimuli successively shown on each trial of the present study differed by 0.5, 1, 1.5, 2, or 2.5° randomly. One stimulus was presented clockwise to the 'standard' orientation, and the other stimulus was presented anti-clockwise to the 'standard' orientation. The 'standard' orientation for a given block of trials was either 25 or 65° anti-clockwise to horizontal (0°). The 40° separation between the two standard orientations was chosen because a recent computational study (Qian & Matthews, 1999), which assumed tuning widths of 40° (full width at half height), predicted that post-training orientation sensitivity would decrease approximately 40° away from the trained orientation<sup>2</sup>. Due to limitations in the monitor's

spatial resolution, jagged edges were present in line stimuli at some orientations. However, these unwanted artifacts, which could have been used as cues to orientation, were significantly reduced by an anti-aliasing feature in the software. Indeed, the anti-aliasing rendered the jagged edges invisible at the distance from which all stimuli were viewed (57 cm). The Michelson contrast of the line stimuli on the orientation-discrimination task was 97%.

On the contrast-detection task, the viewing tube was removed since, unlike orientation judgments, contrast judgments would not be facilitated by external cues to orientation. Additionally, removing the viewing tube allowed a greater amount of ambient light to be reflected from the monitor, thereby permitting a more subtle modulation of luminance contrasts. The Michelson contrast of the line stimulus on the contrast-detection task was 1, 1.75, 2.5, 3.25, or 4%, varying randomly from trial to trial. Within a given block of trials, the line stimulus was always presented at a single 'standard' orientation, either 25 or 65°.

<sup>2</sup> We had considered measuring orientation sensitivity 15° away from the trained orientation, since Regan and Beverley (1985) reported that contrast sensitivity decreased markedly 15° away from the adapted orientation. However, in a pilot study on perceptual learning, we found that training at one orientation did not impair, but instead improved orientation sensitivity 15° away. Likewise, after psychophysically measuring pre-training orientation sensitivity at orthogonal orientations, Schiltz et al. (1999) found that orientation-discrimination training at one orientation significantly enhanced orientation sensitivity 90° away. Consequently, we did not attempt to find orthogonal transfer in the present study.

### 2.2. Observers and experimental procedure

The observers were naive adult humans with normal or corrected-to-normal vision. We began with ten observers. However, three of the ten observers failed to meet our criteria for significant perceptual learning (see below) on the orientation-discrimination task. Because this study was conducted to determine whether significant improvements in orientation sensitivity affected

contrast sensitivity, the three observers who failed to demonstrate significant orientation learning were excluded from data analyses.

The trial sequence for the orientation-discrimination and contrast-detection tasks are, respectively, shown in the top and bottom panels of Fig. 2. On the orientation-discrimination task, observers identified the angular change between the first and second stimuli by rotating the joystick clockwise or anti-clockwise. Clockwise and anti-clockwise orientational changes were presented equally often. Correct orientation judgments could not be made reliably by using positional cues, since the relative position of the two stimuli was randomized independent of the angular difference (Matthews & Welch, 1997). Also, the two stimuli in each orientation-discrimination trial were separated by 600 ms — an interstimulus interval sufficiently long to preclude the use of apparent motion cues. On the contrast-detection task, observers pressed different buttons to indicate whether the line stimulus appeared in the first or second temporal interval. The line stimulus was equally likely to be presented in either interval and the center of the line was randomly positioned about the fixation point, as in the orientation-discrimination task. Auditory feedback was provided after each trial on both tasks. Observers were informed that on both tasks, accuracy was of paramount importance and that reaction time was not being measured. To ensure complete certainty about the ‘standard’ orientation at all times, every trial-block began with a 3 s presentation of a line stimulus indicating the ‘standard’ orientation (either 25 or 65°) for that trial-block.

Our experiment was a within-subjects design, and consisted of a pre-training phase, a training phase, and a post-training phase. The pre-training phase was conducted to determine baselines for both orientation sensitivity and contrast sensitivity. During the training phase, each observer extensively practiced making orientation judgments. The contrast-detection task was not practiced at all during the training phase. In the post-training phase, we again measured orientation sensitivity and contrast sensitivity, for comparison with the baseline. Together, these three phases required a total of 11 daily sessions, which observers typically completed in 2–3 weeks.

### 2.2.1. Pre-training (days 1 and 2)

In the pre-training phase, the orientation-discrimination task was conducted on the first day and the contrast-detection task was conducted on the second. To ensure that each task was understood before baseline sensitivity was measured, observers first completed a worksheet on which trial sequences were schematically drawn. Each observer subsequently practiced supra-threshold trials on the monitor until performance was at least 93% correct. This acquainted the observer

with the stimulus sequence and the required motor response while likely leaving initial discrimination thresholds unaltered.

On each task, every observer completed eight randomly ordered 60-trial blocks, four blocks at each ‘standard’ orientation (25 and 65°). On the orientation-discrimination task, each block comprised 12 randomly ordered presentations of each of the five angular differences (0.5, 1, 1.5, 2, and 2.5°). Similarly, on the contrast-detection task, there were 12 randomly ordered presentations at each of the five luminance contrasts (1, 1.75, 2.5, 3.25, and 4%). For each ‘standard’ orientation, we calculated the observer’s baseline sensitivity ( $d'$ ) to each of the five angular differences (orientation-discrimination task) or luminance contrasts (contrast-detection task). To compute  $d'$  for orientation discrimination, ‘clockwise’ responses to clockwise stimuli were considered Hits, and ‘clockwise’ responses to anti-clockwise stimuli were considered False Alarms. To compute  $d'$  for contrast detection, ‘first-interval’ responses to stimuli presented in the first interval were considered Hits, and ‘first-interval’ responses to stimuli presented in the second interval were considered False Alarms.

### 2.2.2. Training (days 3 through 9)

In the training phase, observers were assigned to a ‘standard’ orientation (either 25 or 65°) according to a counter-balancing procedure. Each observer practiced making orientation judgments around their assigned ‘standard’ orientation for seven daily sessions, with each session comprising six 100-trial blocks. The angular difference between the two stimuli presented on training trials was determined by the observer’s pre-training orientation threshold. Specifically, using the observer’s pre-training data, we plotted the proportion of clockwise responses to orientational changes ranging between 2.5° anticlockwise and 2.5° clockwise, in 0.5° increments. A cumulative normal curve provided an excellent fit to these data ( $P < 0.01$ , in all cases) and could, therefore, be used to fairly estimate the orientation threshold. The orientation threshold was defined as half the angular difference required to alter the response rate from 0.25 to 0.75. This angular difference was presented across the 42 training blocks (six training blocks per session  $\times$  7 daily sessions), and  $d'$  was then calculated for each block.

To demonstrate significant perceptual learning on the orientation-discrimination task, each observer was required to satisfy two criteria during the training phase. First, the mean of the six  $d'$  values obtained from the six blocks in the final training session (day 9) had to be significantly greater than that obtained in the first training session (day 3), according to a  $t$ -test. Second, across the 42 training blocks, the product-moment correlation between orientation sensitivity ( $d'$ ) and practice (i.e. practice block number) had to be significantly

greater than zero. Using these exclusion criteria, we reduced the probability that a null finding on the contrast-detection task (i.e. no difference between pre-training and post-training contrast sensitivity) could be attributed to weak orientation learning.

### 2.2.3. Post-training (days 10 and 11)

The task-sequence in the post-training phase was identical to that in the pre-training phase; orientation discrimination on the first day, and contrast detection on the second. Conducting the tasks in this order extended the number of consecutive sessions (from seven to eight) on which orientation judgments were made, thereby increasing the opportunity to learn on the orientation-discrimination task. Except for the fact that observers in the post-training phase were not required to complete the worksheet that had been administered in the pretraining phase, the post-test and pre-test phases were identical.

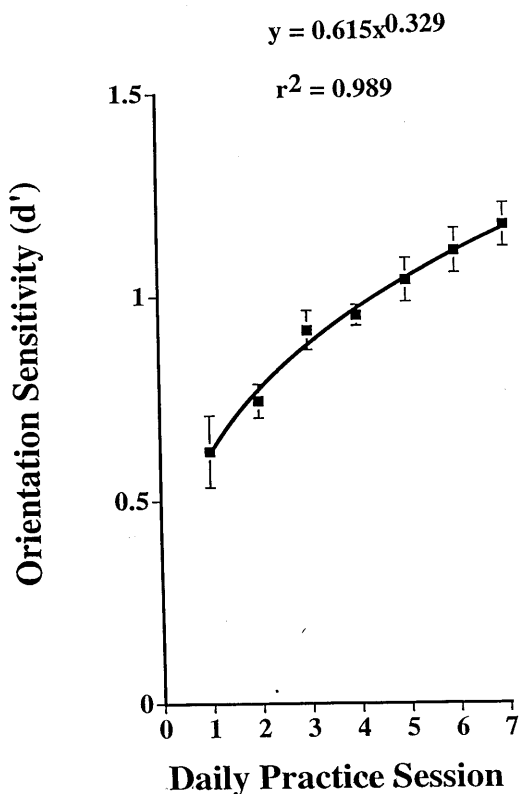


Fig. 3. Perceptual learning during the training phase. Mean orientation sensitivity ( $d'$ ) is plotted as a function of practice. Each datum is based on 4200 trials (7 observers  $\times$  6 practice blocks per day  $\times$  100 trials per block), and error bars reflect one S.E. of the mean after consistent individual differences were removed (Loftus, 1993; Loftus & Masson, 1994). Across the seven training sessions, orientation sensitivity improved significantly from  $d' = 0.63$  to  $d' = 1.17$ . The equation for the best-fitting power function and the proportion of variance explained by that function ( $r^2$ ) are shown.

## 3. Results

Although all observers showed some increase in orientation sensitivity with practice, three observers failed to satisfy our orientation-learning criteria. The results that follow are, therefore, based on data from the seven observers who showed convincing orientation learning, as only these data are relevant to assessing the effect of significant orientation learning on contrast sensitivity.

In Fig. 3, the seven observers' mean orientation sensitivity ( $d'$ ) is plotted for each day of the training phase. With training, mean orientation sensitivity increased from  $d' = 0.63$  (approximately 73% correct) to  $d' = 1.17$  (approximately 88% correct). We found that a power function with an exponent of 0.33 provided an excellent fit to the data, accounting for 98.9% of the variance ( $r(5) = 0.994$ ;  $P < 0.01$ ). These data indicate that significant learning occurred on the orientation-discrimination task during the training phase.

The data from the pre-training and post-training phases of the orientation-discrimination task were evaluated with a  $2 \times 2$  (training by orientation) within-subjects ANOVA. The effect of training was significant, as post-training performance significantly exceeded pre-training performance ( $F(1,6) = 10.67$ ;  $P < 0.025$ ). Both the effect of orientation, and the interaction between training and orientation were non-significant. This suggests that the learning was comparable at the trained and non-trained orientations. Given this comparability, the data from the two orientations were averaged and are plotted in the left panel of Fig. 4. The training effect can be clearly seen across the five angular differences tested, and in the mean.

We found a very similar pattern of results on the contrast-detection data that were taken before and after orientation training. A  $2 \times 2$  (training by orientation) within-subjects ANOVA revealed that contrast sensitivity increased significantly ( $F(1,6) = 9.45$ ;  $P < 0.025$ ) after learning on the orientation-discrimination task. Again, both the effect of orientation, and the interaction between training and orientation were non-significant. Accordingly, data from the two orientations were averaged and are plotted in the right panel of Fig. 4. The increase in contrast sensitivity can be clearly seen across the five luminance contrasts tested, and in the mean. We note also that the increase in contrast sensitivity is not simply an artifact of averaging across observers, since each observer's contrast sensitivity improved after learning occurred on the orientation-discrimination task.

### 3.1. Control experiments

Although the data in Fig. 4 are consistent with the possibility that learning on the orientation-discrimination task improved contrast sensitivity, the same data

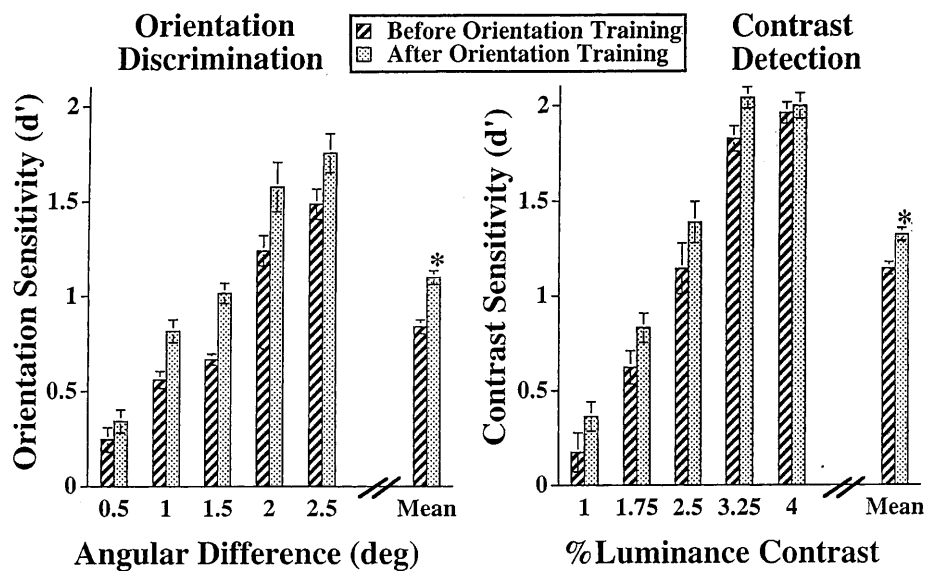


Fig. 4. Pre-training and post-training sensitivity. The observers' mean orientation sensitivity and mean contrast sensitivity are shown in the left and right panels, respectively. The hatched columns reflect pre-training sensitivity, and the dotted columns reflect posttraining sensitivity. Error bars indicate 1 S.E. of the mean after removing consistent individual differences (Loftus, 1993; Loftus & Masson, 1994). At each of the five angular differences tested on the orientation-discrimination task, post-training sensitivity exceeded pre-training sensitivity, and the overall effect of training was significant (far right side of left panel). Similarly, at each of the five luminance contrasts tested on the contrast-detection task, post-training sensitivity exceeded pre-training sensitivity, and the overall effect of training was significant (far right side of right panel).

are also consistent with a simple 'pre-test, post-test effect'. That is, the increase in contrast sensitivity may merely reflect a greater familiarity with the contrast-detection task in the post-training phase, and could be unrelated to the increase in orientation sensitivity. Indeed, it is possible that the orientation training in our main experiment actually reduced contrast sensitivity significantly, but the reduction was masked by a much larger, positive, 'pre-test, post-test effect'. To address this possibility, we conducted a control experiment.

Using the same method and procedures as in the main experiment, we had each of seven new observers complete the contrast-detection task in two different sessions. These sessions were separated by 2–3 weeks, which was the interval separating the pretraining and post-training phases in the main experiment. Observers in the control experiment received no training on the orientation-discrimination task.

We found that, unlike the main experiment, contrast sensitivity in the control experiment increased non-significantly between the first and second sessions ( $F(1,6) = 4.8$ ,  $P > 0.07$ , n.s.). This null finding in the control experiment cannot be explained by a lack of statistical power, since an identical level of statistical power revealed a significant effect in the main experiment. Nor can the null finding in the control experiment be owing to 'floor' or 'ceiling' effects, since the initial mean contrast thresholds were virtually identical in the experimental and control

conditions (1.71 and 1.79% contrast (S.E.  $\pm 0.17\%$ ), respectively). Therefore, the data from the control experiment were not consistent with the notion that orientation training in our main experiment produced contrast-sensitivity reductions that were masked by a much larger 'pre-test, post-test effect'. Indeed, the data from the control condition suggest that while there may be some positive contribution from a 'pre-test, post-test effect', this effect is not sufficient to explain the significant contrast-sensitivity improvements in the main experiment.

The increase in contrast sensitivity after learning on the orientation-discrimination task was unexpected, given Regan and Beverley (1985) finding that adaptation impairs contrast sensitivity while improving orientation sensitivity. One possible explanation for this difference between our results and those of Regan and Beverley, 1985 could be the stimuli. Line stimuli were used in the present study, whereas Regan and Beverley's (1985) used grating stimuli. Grating stimuli were also used in the physiological studies, which indicated that orientation-specific reductions in neural activity accompanied perceptual learning on orientation-discrimination tasks (Ghose & Maunsell, 1997; Schoups et al., 1998; Schiltz et al., 1999). However, it is not obvious why this stimulus difference would matter, particularly since two previous psychophysical studies independently showed that orientation sensitivity is quite comparable for grating and line stimuli (Heeley & Timney, 1988; Westheimer, 1998).

Nevertheless, we had one new naive observer complete our experimental paradigm with grating stimuli, rather than line stimuli. This observer, like those who were tested with line stimuli in our main experiment, demonstrated an increase rather than a decrease in contrast sensitivity after significant orientation learning. Specifically, this observers' contrast thresholds were 1.08% before orientation training, and 0.60% afterwards. Therefore, given this result and the previously demonstrated similarity between line and grating stimuli (Heeley & Timney, 1988; Westheimer, 1998), we believe it is unlikely that the difference between our main finding and Regan and Beverley's (1985) is owing to the choice of stimuli.

#### 4. Discussion

We examined whether perceptual learning on an orientation-discrimination task would subsequently affect performance on a contrast-detection task. Based on previous psychophysical (Regan & Beverley, 1985), physiological (Ghose & Maunsell, 1997; Schoups et al, 1998; Schiltz et al, 1999) and computational (Qian & Matthews, 1999) studies of these tasks, it was hypothesized that a shared underlying cause, such as a reduction in neural activity, could be responsible for adaptation and learning. A prediction from this hypothesis is that improvements in orientation sensitivity should be associated with a decrease in contrast sensitivity. Regan and Beverley (1985) had found precisely such a tradeoff using an adaptation paradigm. Surprisingly, however, the present perceptual-learning paradigm produced a markedly different outcome — practice-based improvements in orientation sensitivity were associated with contrast-sensitivity enhancements, not impairments. We believe the difference between our results and those shown previously by Regan and Beverley (1985) implies that different underlying causes are responsible for perceptual learning and adaptation. An additional prediction was that orientation discrimination should be impaired along an axis away from the trained orientation (about 15° away according to Regan and Beverley (1985) or about 40° away according to our computational model (Qian & Matthews, 1999)). We found no evidence of such an impairment, and this too argued against the hypothesis that perceptual learning and adaptation were mediated by a common underlying cause.

In principle, it is possible that the present improvement in contrast sensitivity after orientation-discrimination training could reflect some general form of learning, rather than a specific modification to orientation sensitivity. Indeed, a general-learning interpretation is consistent with the fact that improvements on both tasks were comparable at the trained and non-

trained orientations, which differed by 40°. However, it is unlikely that the improvements can be entirely explained by an increase in the observers' understanding of the task. This is because on the initial session of each task, the observers' performance increased monotonically with increases in angular difference or luminance contrast (see Fig. 4). Such an orderly dependence on the stimulus suggests a perceptual rather than conceptual performance limit. Moreover, in a previous perceptual learning study (Matthews et al., 1999), we used the same orientation-discrimination training paradigm and stimuli as in the present study, but found that perceptual learning did not generalize from orientation discrimination to direction discrimination. If our orientation-discrimination training paradigm and stimuli produced general learning, one would expect a transfer of learning to various psychophysical tasks (including direction discrimination), not just contrast detection. Indeed, because the orientation-discrimination task and direction discrimination task both required clockwise/anti-clockwise judgments while the contrast-detection task did not, it is surprising that orientation learning transferred to contrast detection but not to direction discrimination.

The null finding in our control experiment suggested that the significant contrast sensitivity increase in our main experiment was not entirely explained by a 'pre-test post-test effect'. This implies that there may have been a partial, positive transfer from orientation sensitivity to contrast sensitivity. Many perceptual learning studies have instead found practice-based improvements to be specific to the trained stimulus (Ramachandran & Braddick, 1973; Fiorentini & Berardi, 1981; Ball & Sekuler, 1987; Fahle, 1997; Fahle & Morgan, 1996) or task (Shiu & Pashler, 1992; Ahissar & Hochstein, 1993)<sup>3</sup>. Suppose that the present training effects had been completely task-specific, i.e. that the significant improvements in orientation sensitivity had absolutely no effect on contrast sensitivity. This hypothetical finding, like our actual finding, would still argue against the possibility that adaptation and perceptual learning arise from a shared underlying cause. To appreciate this point, one must remember that adaptation improves orientation sensitivity while *impairing* contrast sensitivity (Regan & Beverley, 1985). Therefore, after practice-based improvements in orientation sensitivity, any finding other than an impairment to contrast sensitivity would be evidence for a dissimilarity between adaptation and learning. We believe the dissimilarity between

<sup>3</sup> There are very recent exceptions demonstrating a transfer of perceptual learning (Beard, Levi, & Reich, 1995; Ahissar & Hochstein, 1997; De Luca & Fahle, 1999; Liu, 1999; Liu & Vaina, 1995; Liu & Weinshall, 2000; Matthews et al., 1999).

the previous adaptation data (Regan & Beverley, 1985) and the present perceptual-learning data is interesting given the physiological reports, which suggest that perceptual learning (Ghose & Maunsell, 1997; Schoups et al., 1998; Schiltz et al., 1999) and orientation-specific adaptation (Vautin & Berkley, 1977; Movshon & Lennie, 1979; Sclar, Lennie, & DePriest, 1989) are both associated with activity-reductions in V1.

Two previous psychophysical studies provide important insights on the underlying changes that may be responsible for practice-based improvements in orientation discrimination (Burbeck & Regan, 1983; Bradley & Skottun, 1984). Both studies indicated that the ability to see a subtle orientation difference between two gratings is largely independent of whether the gratings are similar or dissimilar in spatial frequency. Therefore, fine orientation-discrimination can occur even when very different populations of neurons are activated by the stimuli being discriminated (Bradley & Skottun, 1984). This suggests that orientation discrimination requires a second stage, which determines the difference between the detecting populations (Westheimer, Shimamura, & Mckee, 1976; Regan & Beverley, 1985). Therefore, practice-based improvements in orientation discrimination could reflect modifications in (second-stage) neurons that are sensitive to the difference between (or ratio of) the activity levels of (first-stage) neurons that detect oriented stimuli.

It is also possible that orientation learning could be explained entirely by modifications to neurons that respond directly to oriented stimuli. For example, practice-induced changes in the steepness of orientation-tuning curves could generate difference-signals larger than those before training (Regan & Beverley, 1985; Qian & Matthews, 1999). These comparatively large post-training difference-signals would enhance orientation discrimination. However, changes in the steepness of orientation-tuning curves could just as easily impair discrimination at orientations displaced from the training orientation, and there are no reports of significant post-training impairments in orientation discrimination. Nor is it obvious how changes in the steepness of orientation-tuning curves would explain the post-training improvements in contrast sensitivity reported here. Alternatively, contrast sensitivity could improve if practice on an orientation-discrimination task were to reduce variability in the response of orientation-tuned neurons. Electrophysiological recordings taken before and after practice-based improvements in orientation discrimination, however, revealed no such reduction in the response variability of orientation-tuned neurons (Schoups et al., 1998). Lastly, we note another possibility, which derives from the finding that the response of orientation-tuned neurons scales in a task-relevant manner (McAdams & Maunsell, 1999a,b). As a speculation, it may be that rather than a simple reduction of

firing rates, training on orientation discrimination enhances the extent to which visual neurons can decrease or increase firing in a task-relevant manner. Specifically, after orientation learning, a neuron tuned to the trained orientation might fire less to the high-contrast oriented stimuli used in the orientation-discrimination task but fire more to the low-contrast oriented stimuli used in the contrast-detection task. Such a change in capacity could enable the neuron to reduce its activity when its response does not contribute to an orientation judgment, and increase its activity when its response provides optimal information for detecting a faint stimulus. In any event, if extensive orientation-training were to induce, instead, a task-independent decrease in the firing rates of particular visual neurons, any resulting enhancement to orientation sensitivity would likely come at the expense of contrast sensitivity. This would be a costly trade-off for an organism, and our data suggest that visual system does not make such a trade-off.

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### References

- Ahissar, M., & Hochstein, S. (1993). Attentional control of early perceptual learning. *Proceedings of the National Academy of Sciences*, 90(12), 5718–5722.
- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, 387, 401–406.
- Ball, K., & Sekuler, R. (1987). Direction specific improvements in motion discrimination. *Vision Research*, 27(6), 953–965.
- Beard, B. L., Levi, D. M., & Reich, L. N. (1995). Perceptual learning in parafoveal vision. *Vision Research*, 35, 1679–1690.
- Bradley, A., & Skottun, B.C. (1984). The effects of large orientation and spatial frequency differences on spatial discriminations. *Vision Research*, 24 (12), 1889–1896.
- Burbeck, C. A., & Regan, D. (1983). Independence of orientation and size in spatial discriminations. *Journal of the Optical Society of America*, 73(12), 1601–1694.
- Carandini, M., & Ringach, D. L. (1997). Prediction of a recurrent model of orientation selectivity. *Vision Research*, 37, 3061–3071.
- Chen, S., & Levi, D. M. (1996). Meridional anisotropy in the discrimination of parallel and perpendicular lines — effect of body tilt. *Perception*, 25(6), 633–649.
- De Luca, E., & Fahle, M. (1999). Learning of interpolation in two- and three-dimensions. *Vision Research*, 39(12), 2051–2062.
- Dosher, B. A., & Lu, Z. L. (1999). Mechanisms of perceptual learning. *Vision Research*, 39, 3197–3221.
- Fahle, M. (1997). Specificity of learning curvature, orientation, and vernier discriminations. *Vision Research*, 37(14), 1885–1895.



- Fahle, M., & Morgan, M. (1996). No transfer of perceptual learning between similar stimuli in the same retinal position. *Current Biology*, 6(3), 292–297.
- Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination; specificity for orientation and spatial frequency. *Vision Research*, 21, 1149–1158.
- Geesaman, B. J., & Qian, N. (1996). A novel speed illusion involving expansion and rotation patterns. *Vision Research*, 36(20), 3281–3292.
- Ghose, G. M., & Maunsell, J. H. R. (1997). Perceptual learning can selectively alter neural responses in primate V1. *Society for Neuroscience Abstracts*, 23(2), 1544.
- Heeley, D. W., & Timney, B. (1988). Meridional anisotropies of orientation discrimination for sine wave gratings. *Vision Research*, 28(2), 337–344.
- Liu, Z. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. *Proceedings of the National Academy of Sciences USA*, 96(24), 14085–14087.
- Liu, Z., & Vaina, L. M. (1995). Stimulus-specific learning: a consequence of stimulus-specific experiments? *Perception*, 24(Suppl.), 21.
- Liu, Z., & Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research*, 40(1), 97–109.
- Loftus, G. R. (1993). A picture is worth a thousand *p* values: on the irrelevance of hypothesis testing in the microcomputer age. *Behavior Research Methods Instruments and Computers*, 25(2), 250–256.
- Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subjects designs. *Psychonomic Bulletin and Review*, 1(4), 476–490.
- Matthews, N., & Welch, L. (1997). Velocity-dependent improvements in single-dot direction discrimination. *Perception and Psychophysics*, 59(1), 60–72.
- Matthews, N., Liu, Z., Geesaman, B. J., & Qian, N. (1999). Perceptual learning on orientation and direction discrimination. *Vision Research*, 39(22), 3692–3701.
- McAdams, C. J., & Maunsell, J. H. R. (1999a). Effects of attention on orientation-tuning functions of single neurons in Macaque cortical area V4. *The Journal of Neuroscience*, 19(1), 431–441.
- McAdams, C. J., & Maunsell, J. H. R. (1999b). Effects of attention on the reliability of individual neurons in monkey visual cortex. *Neuron*, 23(4), 765–773.
- McCollough, C. (1965). Color adaptation of edge-detectors in the human visual system. *Science*, 149, 1115–1116.
- Movshon, J. A., & Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature*, 278(5707), 850–852.
- Orban, G. A., & Vogels, R. (1998). The neuronal machinery involved in successive orientation discrimination. *Progress in Neurobiology*, 55, 117–147.
- Qian, N., & Matthews, N. (1999). A physiological theory for visual perceptual learning of orientation discrimination. *Society for Neuroscience Abstracts*, 25(2), 1316.
- Ramachandran, V. S., & Braddick, O. (1973). Orientation specific learning in stereopsis. *Perception*, 2, 371–376.
- Regan, D., & Beverley, K. I. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America A*, 2(2), 147–155.
- Rivest, J., Boutet, I., & Intriligator, J. (1997). Perceptual learning on more than one attribute. *Vision Research*, 37(3), 273–281.
- Schiltz, C., Bodart, J. M., Dubois, S., Dejardin, S., Michel, C., Roucoux, A., Crommelinck, M., & Orban, G. A. (1999). Neuronal mechanisms of perceptual learning: changes in human brain activity with training in orientation discrimination. *Neuroimage*, 9(1), 46–62.
- Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: retinotopy, orientation specificity and monocularly. *Journal Physiology*, 483, 797–810.
- Schoups, A. A., Vogels, R., & Orban, G. A. (1998). Effects of perceptual learning in orientation discrimination on orientation coding in V1. *Investigative Ophthalmology and Visual Science Supplement*, 39(4), s684.
- Sclar, G., Lennie, P., & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research*, 29(7), 747–755.
- Shiu, L., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception and Psychophysics*, 52(2), 582–588.
- Somers, D. C., Nelson, S. B., & Sur, M. (1995). An emergent model of orientation selectivity in cat visual cortical simple cells. *Journal of Neuroscience*, 15, 5448–5465.
- Vautin, R. G., & Berkley, M. A. (1977). Response of single cells in cat visual cortex to prolonged stimulus movement: neural correlates of visual aftereffects. *Journal of Neurophysiology*, 40(5), 1051–1065.
- Vogels, R., & Orban, G. A. (1985). The effect of practice on the oblique effect in line orientation judgments. *Vision Research*, 25, 1679–1687.
- Westheimer, G. (1998). Lines and gabor functions compared as spatial visual stimuli. *Vision Research*, 38(4), 487–491.
- Westheimer, G., Shimamura, K., & Mckee, S. P. (1976). Interference with line orientation sensitivity. *Journal of the Optical Society of America*, 66(4), 332–338.