Physiological Correlates of Perceptual Learning in Monkey V1 and V2

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J Neurophysiol 87: 1867–1888, 2002; 10.1152/jn.00690.2001. Performance in visual discrimination tasks improves with practice. Although the psychophysical parameters of these improvements have suggested the involvement of early areas in visual cortex, there has been little direct study of the physiological correlates of such perceptual learning at the level of individual neurons. To examine how neuronal response properties in the early visual system may change with practice, we trained monkeys for more than 6 mo in an orientation discrimination task in which behaviorally relevant stimuli were restricted to a particular retinal location and oriented around a specific orientation. During training the monkeys' discrimination thresholds gradually improved to much better than those of naive monkeys or humans. Although this improvement was specific to the trained orientation, it showed little retinotopic specificity. The receptive field properties of single neurons from regions representing the trained location and a location in the opposite visual hemifield were measured in V1 and V2. In most respects the receptive field properties in the representations of the trained and untrained regions were indistinguishable. However, in the regions of V1 and V2 representing the trained location, there were slightly fewer neurons whose optimal orientation was near the trained orientation. This resulted in a small but significant *decrease* in the V1 population response to the trained orientation at the trained location. Consequently, the observed neuronal populations did not exhibit any orientation-specific biases sufficient to explain the orientation specificity of the behavioral improvement. Pooling models suggest that the behavioral improvement was accomplished with a task-dependent and orientation-selective pooling of unaltered signals from early visual neurons. These data suggest that, even for training with stimuli suited to the selectivities found in early areas of visual cortex, behavioral improvements can occur in the absence of pronounced changes in the physiology of those areas.

INTRODUCTION

The improvement of sensory abilities with practice has been demonstrated for somatosensory, auditory, and visual stimuli in both animals and humans (Goldstone 1998). Studies of neurons in primary auditory and somatosensory cortex have revealed training-related changes in both the mapping of response properties across the cortical surface and the sensitivities of individual neurons. These changes suggest that adult cortex is remarkably plastic; training can increase the number of neurons whose selectivities correspond to the demands of the training task (Jenkins et al. 1990a; Recanzone et al. 1993) and can increase neuronal selectivity (Recanzone et al. 1992b).

In primary visual cortex (V1) plasticity of neuronal response properties has also been observed during the course of normal development (Chapman and Stryker 1993; Crair et al. 1998; DeAngelis et al. 1993; Fregnac and Imbert 1978; Ghose et al. 1994b; LeVay et al. 1980; Sclar et al. 1985), in response to environmental modifications including monocular deprivation (Blakemore et al. 1978, 1981; Cynader et al. 1980; Hubel and Wiesel 1965; Hubel et al. 1977; Olson and Freeman 1978, 1980; Shatz and Stryker 1978; Swindale et al. 1981; Wiesel and Hubel 1965a,b) and ocular misalignment during development (Chino et al. 1991, 1994; Kumagami et al. 2000; Sasaki et al. 1998). Plasticity in adult visual cortex has been shown in response to localized deafferentation by retinal lesioning (Chino et al. 1992, 1995; Gilbert and Wiesel 1992; Heinen and Skavenski 1991; Kaas et al. 1990). Yet few studies have addressed how neuronal properties in adult V1 change as a consequence of training. This is clearly important in order to understand whether the changes that have been reported in other modalities reflect a general property of sensory cortices. Moreover, visual cortex is an ideal arena for examining these changes for a number of reasons. First, our understanding of the synaptic (Adrien et al. 1985; Bear and Daniels 1983; Bear and Singer 1986; Bear et al. 1983; Carmignoto et al. 1993; Ghose et al. 1994a; Gu and Singer 1993; Hendry and Jones 1986; Kleinschmidt et al. 1987; Maffei et al. 1992; Ramoa et al. 1988; Speed et al. 1991) and anatomical (Antonini and Stryker 1993, 1996; Elliott et al. 1996; Kossel et al. 1995) aspects of such plasticity is more advanced for visual cortex than it is for any other sensory cortical area. Second, the anatomy, functional architecture, and receptive field selectivities of adult visual cortex are well characterized. Third, many studies have demonstrated improvements in visual discrimination with practice. The relatively sophisticated understanding of vision both physiologically and psychophysically enables a more detailed examination of correlations between behavior and physiology than is possible for other modalities. For example, the observed changes in other sensory cortices have been associated with parameters that are mapped among the inputs to the cortex: frequency in the case of auditory cortex and somatotopy in the case of somatosensory cortex. Neurons in visual cortex are robustly selective for many parameters that do not correspond with receptor surface (retinotopy), including orientation, spatial frequency, color, and disparity. Moreover, the early stages of visual cortex offer the opportunity to examine how training affects cortical processing specifically because several of these visual selectivities, including orientation and binocularity, first appear at the level of cortex.

To study the physiological correlates of perceptual learning in the early visual system, we trained two macaques to discriminate fine changes in orientation at a specific location in

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the visual field and around a fixed orientation. We then measured the response properties of cells in V1 and V2 that represented trained or untrained locations. Both animals showed considerable behavioral improvement with training. In contrast to studies in auditory and somatosensory cortex, we found only small location- and orientation-specific effects on neuronal responses. These results suggest that changes in early visual cortex may not underlie the behavioral improvements that arise from such training.

METHODS

Behavioral training

Two adult monkeys (*Macaca mulatta*) were first trained to discriminate orthogonally oriented stimuli in a match to sample task. During this initial training the animals sat unrestrained in a primate chair for daily training sessions that lasted from 2 to 4 h. At other times the animals were unrestrained in primate cages and food was provided ad libidum, but liquid consumption was restricted to the training session in which juice or water rewards were given for correctly performed trials. Visual stimulation and behavior control were computer controlled. Stimuli were presented on a video display on a gray background (15.6 cd/m^2, CIE $x = 0.33$, $y = 0.33$). Each gun of the display was gamma-corrected for 256 (8 bit) levels. Stimuli were achromatic sinusoidally counter-phasing Gabors (temporal frequency = 3 or 4 Hz; spatial frequency = 2 cycles/deg, $\sigma = 0.5°$) that were oriented either horizontally and vertically during this phase of the training. Trials consisted of a presentation of a sample stimulus followed by a 500-ms delay and then a test stimulus. Trials began when the monkey depressed a lever mounted in front of the chair in response to the appearance of a Gabor. The monkeys' task was to indicate whether the subsequently presented Gabor differed in orientation by releasing or not releasing the lever. Matching and nonmatching trials occurred equally often in a random sequence. One animal was required to release the lever for matches; the other animal had to release for nonmatches.

Once the monkeys learned to discriminate nonmatching stimuli that differed by 90°, the spatial frequencies of the stimuli were gradually changed over the course of several weeks such that the sample and test stimuli were of different spatial frequencies on each trial. This behaviorally irrelevant change in spatial frequency was introduced for several reasons. First, it made the task more demanding. Second, it reduced the chance that positional clues such as spatial phase could be used to solve the task. Third, because only two spatial frequencies were used, it provided a control for the effects of repeated exposure: any differences seen in response properties with respect to orientation that are not present with respect to spatial frequency cannot be explained simply by repeated exposure to the stimulus. Fourth, because most single neurons in the visual cortex are selective for both orientation and spatial frequency, it ensured that the task would either involve groups of neurons or would create neurons with fundamentally different response selectivities (i.e., bimodal or unusually broad spatial frequency tuning). In either case, the chances of detecting such a change would be larger than if the task could potentially be solved by the signals produced by a small number of normal neurons in visual cortex. Finally, it allowed us to examine potential correlates of attribute-selective training since the monkeys had to learn to ignore spatial frequency differences that were readily discriminable while attending to barely discernible changes in orientation.

After the monkeys performed this orientation task at a 90% correct for stimuli of 1 and 4 cycles/deg, a head post and scleral search coil were surgically implanted. After a 2-wk recovery period, the monkeys were trained to fixate. Once the animals could maintain fixation for 1.5 s within a square 1.2° across, location-specific training was begun using Gabors presented in the lower right quadrant at 3° eccentricity

and 30° from the vertical meridian. These trials began when the monkey fixated on a small dot (0.1°) on the screen and depressed the lever. Sample stimuli were presented for 500 ms following an initial 500-ms prestimulus period. In *monkey 2,* 17 behaviorally irrelevant Gabors (distractors) were also presented in other locations during the sample and test periods. The distractor Gabors had random orientations, spatial frequencies, and temporal phases. The 18 Gabors (17 distractors + 1 training Gabor) were arranged in a regular grid at eccentricities 1.5, 3.0, and 6.0° with an angular interval of 60°. The Gabors were scaled for eccentricity: σ was 0.25, 0.5, and 1.0° for the different eccentricities. For the monkey in which distractors were used, the gradual reduction of orientation difference at the training location was only begun after the monkey performance with full contrast distractors was around 95%. For the next 5–6 mo, orientation differences were gradually reduced so that the average correct performance in a daily session was no less than 75%.

Electrophysiological recording

When the training was complete, a second surgery was performed to implant a recording chamber over the portions of V1 and V2 representing the trained location. Maintenance of the trained threshold was verified by presenting 100–200 training trials to the monkeys at the beginning of each recording session before any electrophysiological recording. While neurophysiological data were being recorded, the monkey performed a different match-to-sample task using pairs of diagonally oriented fine lines (length 0.2°) surrounding the fixation point (eccentricity ~0.1°). Eye movements were minimal since the behavioral task was at the fixation point, and the peripherally presented stimuli were behaviorally irrelevant. In one of the animals, eye position data were acquired for both the fixation and the trained task. In this animal the average eye position difference between the two tasks was 0.14°.

The monkey's task was to use the lever to indicate whether the lines presented in the test period matched those of the sample period. Nonmatching lines differed by 90° in orientation. The timing of the sample and test stimulus presentations was the same as was used for the peripheral orientation discrimination training. Performance on this task was above 95%. Response properties of neurons were recorded using behaviorally irrelevant stimuli presented at the receptive field location during both the sample and test periods.

Single neurons in V1 were recorded extracellularly using transdural Pt-Ir electrodes (~1 MΩ). To reduce selection bias while searching for cells, gratings of all orientations were presented in random interleaved sequences (Ringach et al. 1997). The timing of action potentials from isolated neurons and presentation of visual stimuli were recorded with 1-ms resolution. Eye position and lever movements were recorded with 5-ms resolution.

Once a single unit was isolated, its receptive field position, optimal orientation, and optimal spatial frequency were initially estimated by presenting Gabors with manually chosen parameters. After this initial estimate, Gabors were presented in computer-controlled randomly interleaved sequences to quantitatively measure response properties. Orientation selectivity was assessed using a fixed set of eight different orientations (22.5° increments). The optimal orientation was then used to measure selectivity for spatial frequency and size (σ of the Gaussian envelope describing the Gabor). If any of these subsequent runs revealed an optimal parameter appreciably different from the initial estimate, orientation tuning was reexamined with the new optimal parameter (approximately 20% of neurons). Stimulus centering with respect to receptive field position was verified by ensuring that neurons responded to optimal stimuli whose σ was 0.1°. To facilitate comparisons between different cells, all parameters were varied over consistent ranges: spatial frequency from 0.5 to 8 cycles/deg (octave increments); size from 0.1 to 0.5°. All tests included 12 repetitions of 500-ms presentations.

Identical methods were used for recording from the trained and

untrained representations in V1 and V2. For studying the untrained representations in V1 and V2, a second recording chamber was mounted over the opposite hemisphere. For each recording region, approximately 100 cells from each animal were recorded with 23 to 45 electrode penetrations. About one-half of the V2 penetrations were done with transdural electrodes; in the remaining penetrations, guide tubes were used to penetrate the dura.

For *monkey 2,* after chronic and behavior testing was completed, multiunit activity in the trained hemisphere was recorded in an acute experiment in which recordings were made in an anesthetized (sufentanil) and paralyzed (vercuronium) preparation. No acute mapping was done in *monkey 1* because the trained representation of V1 was unexpectedly damaged during V2 recording. Procedures for animal preparation and maintenance have been detailed elsewhere (Maunsell et al. 1999). Vertical penetrations were made at regular 1-mm intervals along a grid spanning the representation of the trained region in V1 and V2. Monocular multiunit receptive fields were plotted on a tangent screen using a hand-held projector. For each penetration, receptive field boundaries were confirmed by plotting receptive fields at two or more sites separated by at least 200 μm.

Behavioral testing

After neurophysiological data had been collected from trained and untrained regions in V1 and V2, extended psychophysical testing of orientation discrimination performance was done. Orientation discrimination thresholds were measured at an untrained location 3° from the vertical meridian in the lower left quadrant. For *monkey 1,* discrimination thresholds were determined by measuring performance to various orientation changes and taking the orientation difference associated with 79% performance on a fitted exponential sigmoid. For *monkey 2,* thresholds were measured by a staircase procedure that converged at a performance level of 79%. The staircase procedure was repeated to give an estimate of the variability of performance. Because of the aforementioned V1 damage in *monkey 1,* we were unable to obtain behavioral thresholds for nontrained stimuli at the trained location in that animal. However, for *monkey 2,* we evaluated the orientation specificity of the behavioral improvement. Probe trials were randomly inserted within a standard discrimination training run. For such trials, the monkey's task was the same peripheral orientation discrimination task that was trained, except that the base orientation around which stimuli were oriented and the orientation difference between nonmatching stimuli were varied.

Electrophysiological analysis

DESCRIPTIVE FUNCTIONS. Response functions for orientation, spatial frequency, and size (Table 2) were fit using a maximum likelihood method (Geisler and Albrecht 1997). Orientation responses were modeled by a wrapped Gaussian (Swindale 1998), and spatial frequency and size were modeled by symmetric Gaussians. Maximum-likelihood fits were obtained using measured spike count means and by assuming variance to be proportional to the mean (Geisler and Albrecht 1997).

The proportionality of variance to mean (K) was determined using orientation measurements because these had the greatest number of stimuli tested (8 orientations). Thus for orientation, five parameters were obtained by descriptive function fit: baseline firing rate, peak firing rate, tuning bandwidth, peak orientation, and the proportionality of variance constant (K). For the spatial frequency and size tuning runs, four parameters were obtained: baseline firing rate, peak firing rate, tuning bandwidth, and peak position. To test for the effects of orientation and location-specific effects, we looked for correlations between descriptive function parameters and preferred orientation as well as correlations between these parameters and receptive field location. For tuning amplitude and peak response, all statistical analyses were done on log-transformed data. To examine dependence on

preferred orientation, vectors were constructed in which the amplitude was the parameter of interest (orientation bandwidth, for example), and the angle was the cell's preferred orientation. The distribution of these vectors was analyzed for angular biases by computing the centroid confidence region for the vectors and determining the likelihood that the origin lay within this region (Hotelling test) (Batschelet 1981). For response measures such as tuning magnitude, a nonparametric rank-weighted test was also used to find angular bias (Moore test) (Batschelet 1981). For all parameters, circular regression analysis was used to examine the dependence on preferred orientation (C-association test) (Fisher 1996). To look for parameter dependence on position, the correlation coefficient between each parameter and the receptive field distance from the center of the training stimuli was computed.

To simultaneously test for changes related to training orientation and location, parameters were grouped according to location (trained location vs. untrained location) and orientation (trained orientation vs. untrained orientation) and tested by ANOVA. For these groups, cells were classified as belonging to the trained location group if their receptive field center was located within 1.5σ (0.75°) of the center of the training stimuli and as belonging to the trained orientation group if their preferred orientation was within 11.25° of the training orientation (45°). For all statistical tests, a criterion value of $P = 0.01$ was used.

DETECTION THEORY. To relate the physiological observations to performance in the task, we evaluated the performance of an ideal observer of the neuronal responses to the training stimuli. Because we typically did not record from neurons while the animal performed the discrimination task, we inferred the responses to our training stimuli using fitted descriptive functions of orientation and spatial frequency and assuming that the selectivities for these two parameters are separable. Specifically, we constructed two orientation tuning curves for 1 and 4 cycles/deg based on ratios derived from the spatial frequency tuning curve and the orientation tuning curve acquired at the preferred spatial frequency.

Two types of ideal observer models were tested: a discrimination model and a classification model. In the first, discriminability describes how well two sets of neuronal responses can be distinguished using an optimal threshold (Fig. 11, *A* and *C*). The discriminability (d') between two signal distributions of unequal variances is described by the means (μ) and the variances (σ^2) of the two distributions (Green and Swets 1988)

$$d' = \frac{\mu_1 - \mu_2}{\sqrt{\dfrac{\sigma_1^2 + \sigma_2^2}{2}}}$$

In our case, the distributions to be compared are the responses when an orientation change occurs (nonmatch) and when no change occurs (match). So the match signal for the high orientation, low spatial frequency sample is

$$\mu_1 = \mu_{\text{match}} = r(\theta = \theta_0 + \delta, f = 1) - r(\theta = \theta_0 + \delta, f = 4) \text{ and } \sigma_1^2 = K \cdot \mu_1$$

and the nonmatch signal for the same sample is

$$\mu_2 = \mu_{\text{nonmatch}} = r(\theta = \theta_0 + \delta, f = 1) - r(\theta = \theta_0 - \delta, f = 4) \text{ and } \sigma_2^2 = K \cdot \mu_2$$

where θ_0 is the orientation around which training occurred (45°), δ is one-half of the orientation difference, and K is proportionality of means and variances. All responses and variances were computed using the aforementioned descriptive functions.

Because the monkeys could perform well in sessions where the orientation difference was continually adjusted (δ is not constant), the remembered stimuli of any comparison would have to correspond to the responses elicited at the trained orientation θ_0 so that

$$\mu_{\text{match}} = [r(\theta = \theta_0 + \delta, f = 1) - r(\theta = \theta_0, f = 1)]$$

$$- [r(\theta = \theta_0 + \delta, f = 4) - r(\theta = \theta_0, f = 4)]$$

and

$$\mu_{\text{nonmatch}} = [r(\theta = \theta_0 + \delta, f = 1) - r(\theta = \theta_0, f = 1)]$$
$$- [r(\theta = \theta_0 - \delta, f = 4) - r(\theta = \theta_0, f = 4)]$$

Note that in all of these cases the difference in the means reduces to the difference seen in a matched spatial frequency comparison

$$\mu_{\text{match}} - \mu_{\text{nonmatch}} = r(\theta = \theta_0 + \delta, f = 1) - r(\theta = \theta_0 - \delta, f = 1)$$

Thus discrimination is based not on a direct comparison between sample and test, but rather a comparison of sample and test stimuli to a criterion response corresponding to a stimulus ($\theta = \theta_0$), which is not actually presented but lies in the middle of the range of presented stimuli (Lages and Treisman 1998) (Fig. 11*A*). For these purposes we assume a perfect memory of the responses to all the stimuli that were presented as well as the reference stimuli ($\theta_0 = 45°$).

In the second ideal observer model, each stimulus response is classified as being above or below the training orientation (Fig. 11, *B* and *D*). Such a classification depends on the range of responses produced by the presented stimulus and the total range of responses for all stimuli. In this respect it differs from discrimination, which involves the comparison of the responses to two specific orientations. So for the same high orientation, low spatial frequency sample the probability that it will be classified as above θ_T is

$$p(\theta > \theta_T, f = 1 | \theta_{\text{sample}} = \theta_T + \delta, f = 1)$$
$$= \int_{\theta' > \theta_T} \int_{R'} p(\theta' | R') \cdot p(R' | \theta = \theta_T + \delta, f = 1) dR' d\theta'$$

Assuming that responses are normally distributed the probability of an orientation θ given a response R is

$$p(\theta | R) = \frac{p(R | \theta)}{\int p(R | \theta') d\theta'}$$

and the probability of a response r given an orientation θ is

$$p(R | \theta) = \frac{1}{\sqrt{2\pi K r(\theta)}} \exp\left\{ -\frac{[R - r(\theta)]^2}{2K r(\theta)} \right\}$$

For example, a cell whose peak orientation is θ_T with zero response variance ($K = 0$) will have a 50% chance of correct identification since the response to $\theta_T + \delta$ is equally likely to have come from $\theta_T - \delta$ as from $\theta_T + \delta$ (Fig. 11*B*). A decision is then based on the classifications of both the sample and test stimulus. So the probability of detecting an orientation match depends on both the sample and match being classified correctly or both the sample and match being classified incorrectly

$$p(\text{match}) = p(\text{sample, correct}) \cdot p(\text{test, correct})$$
$$+ p(\text{sample, wrong}) \cdot p(\text{test, wrong})$$

For the orientation matching trial with the high orientation, low spatial frequency sample used above

$$p(\text{match} | \theta_{\text{sample}}, \theta_{\text{test}}) = p(\theta > \theta_T | \theta_{\text{sample}}, f = 1) \cdot p(\theta > \theta_T | \theta_{\text{test}}, f = 4)$$
$$+ p(\theta < \theta_T | \theta_{\text{sample}}, f = 1) \cdot p(\theta < \theta_T, \theta_{\text{test}}, f = 4)$$

where

$$\theta_{\text{sample}} = \theta_{\text{test}} = \theta_T + \delta$$

RESULTS

Perceptual learning

Throughout training the orientation difference was reduced whenever the animals were performing at 80% correct for 200–400 trials. Within several days, the orientation difference

was reduced from 90° to about 15–20° around an orientation of 45°, which is roughly the range in which naive humans perform this task (Fig. 1). Further reductions in the orientation discrimination threshold occurred more slowly, such that a threshold of 4–5° was reached only after about 6 mo of training (~100,000 correct trials). Behavioral improvements were well modeled by single exponentials. This pattern of slowing improvement is similar to that seen in monkeys during tactile discrimination training (Recanzone et al. 1992a).

Behavioral performance for untrained locations and orientations was measured after all recordings had been completed. For both animals, performance was measured for stimuli presented at an untrained location directly across the vertical meridian from the trained location. Orientation was varied around both the trained orientation (45°) and an untrained orientation (135°). For *monkey 2* performance was also measured for an untrained orientation (135°) at the trained location. All performance was measured in the absence of any distractors.

In both animals learning was orientation specific (Table 1): orientation discrimination thresholds at both locations were poorer for stimuli varying around an untrained orientation and
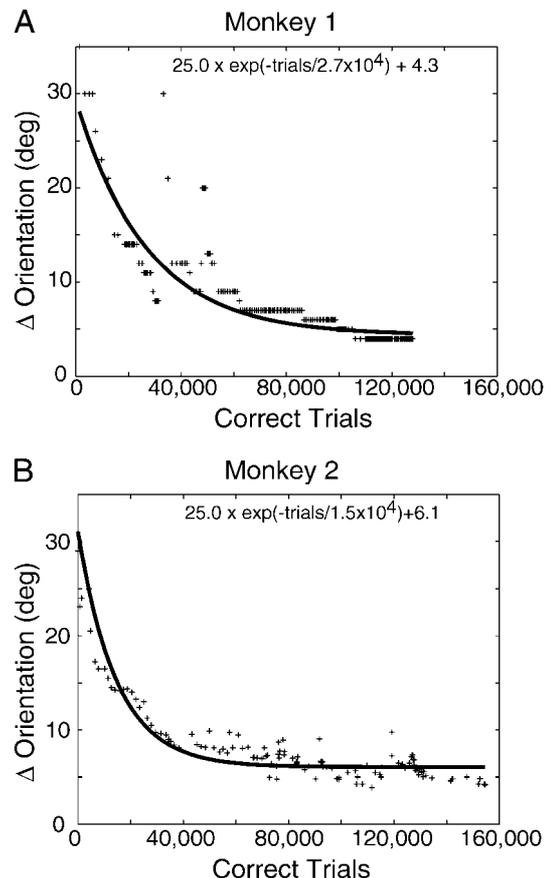

FIG. 1. Orientation discrimination thresholds as a function of training in 2 macaques. The training of *monkey 1* is shown in *A,* and the training of *monkey 2* is shown in *B*. Each point indicates the average orientation difference of nonmatching trials in a daily recording session, which typically included 1,000–2,000 correct trials during the initial training. Thresholds were adjusted to maintain a performance of 75–80% correct trials. In both animals, initial training produced rapid changes in threshold. Reduction of threshold after 40,000 correct trials was considerably slower. The thresholds were fit by a single exponential, indicating asymptotic thresholds at 4.3 and 6.1° for the 2 monkeys.

TABLE 1. *Discrimination thresholds as a function of orientation and location*

| | Monkey 1 | | Monkey 2 | |
| | | | | |
Location	Trained orientation (45°)	Untrained orientation (135°)	Trained orientation (45°)	Untrained orientation (135°)
Trained	3.3		7.3 ± 0.59	27.4 ± 2.1
Untrained	6.3	16.8	11.0 ± 1.0	38.4 ± 2.7

Values for *monkey 2* are means ± SE.

were similar to thresholds observed at the beginning of training (Fig. 1). In contrast, there was a much smaller effect of retinotopic position: orientation thresholds in the untrained location were similar to those seen in the trained location. The trained-orientation/untrained-location threshold was much lower than the trained-location/untrained-orientation threshold. The psychophysical data therefore indicate that despite orientation- and location-specific training, perceptual improvements were orientation specific but only marginally location specific. This is particularly notable for *monkey 2,* because the untrained location corresponded to the location of a distractor that had to be ignored during the course of training.

Single-cell receptive field properties

Orientation tuning curves were acquired from 867 cells in two animals. Spatial frequency and optimal size tuning was evaluated for 775 and 651 of these cells, respectively (Table 3). Only cells whose receptive fields overlapped the training stimuli (RF centers within 1.5σ of the center of the training stimuli) were included in the trained population. Cells from the trained hemisphere outside of this border were excluded from analysis. Figure 2 shows cumulative distributions of cells in the trained hemisphere (dashed lines) and cells within the trained location (solid lines) for V1 and V2. Of the 169 V1 cells in the trained hemisphere, 139 were accepted for analysis; of the 153 V2 cells, 129 were accepted.

Figure 3 shows the responses and fitted descriptive functions for one cell from the trained V1 population and another cell from the untrained V1 population. Solid lines indicate the fitted functions for mean firing rates. Tuning curves were considered well fit when the correlation coefficient between the observations of response means and the fitted model was at least 0.80. For each neuronal population, approximately 75% of the functions met this criterion (Table 3). Among well-fit tuning curves, the average correlation coefficient for orientation was 0.93, and for spatial frequency and size was 0.96 in both V1

TABLE 2. *Descriptive response functions*

Response mean	$r = r_{max} \cdot r(x) + r_0$
Response variance	$V = K \cdot r$
Orientation	$r_\theta(\theta) = \sum_n \exp\left[-\frac{(\theta - \theta_c + 180n)^2}{b_\theta^2} \right]$
Spatial frequency	$r_f(f) = \exp\left[-\frac{(f - f_c)^2}{b_f^2} \right]$
Size	$r_\sigma(\sigma) = \exp\left[-\frac{(\sigma - \sigma_c)^2}{b_\sigma^2} \right]$

TABLE 3. *Number of tuning curves (number of well-fit curves)*

Area	Location	Orientation	Spatial Frequency	Size
V1	Trained	214 (169)	183 (143)	137 (99)
	Untrained	235 (180)	216 (163)	183 (131)
V2	Trained	194 (153)	174 (130)	157 (114)
	Untrained	224 (170)	202 (143)	174 (130)

and V2 populations. The mean parameters in all neuronal populations were consistent with those reported by Geisler and Albrecht (1997) using similar methods.

Receptive field properties were similar between trained and untrained populations and between trained and untrained orientations. Most receptive field properties did not depend on either receptive field location or preferred orientation. In the few cases in which significant differences were present, there were small and not obviously consistent with the pattern of improved performance (Table 1). The remainder of this section details the analyses used to examine the dependence of receptive field properties on location and orientation.

Preferred orientation distributions were compiled for each of the four neuronal populations (Fig. 4). In both animals there was a small but significant bias in the distribution of preferred orientations (Raleigh test, $P < 0.005$) in the V1 population representing the trained location (Fig. 4A). Unexpectedly, there were significantly fewer cells whose preferred orientations were near the trained orientation (45°) than would be expected with an unbiased distribution (V-test, $P < 0.005$). A similar trend was seen in the V2 trained population (*B*), but it was not statistically significant. No significant biases with respect to orientation were seen in the untrained populations (*C* and *D*).

Preferred orientation distributions were also computed using all cells within the trained and untrained regions irrespective of the quality of their orientation fit (not shown). In one analysis, the preferred orientation of cells with well-fit orientation functions was taken from the function maximum, and the preferred orientation of the remaining cells was taken as the orientation that evoked the greatest response. In another analysis, the orientation that evoked largest response was used for all cells. For all the statistical analyses, these two methods yielded identical results as the distributions shown in Fig. 4.

Changes in preferred orientation is only one of the possible changes that might result from training. Orientation discrimi-
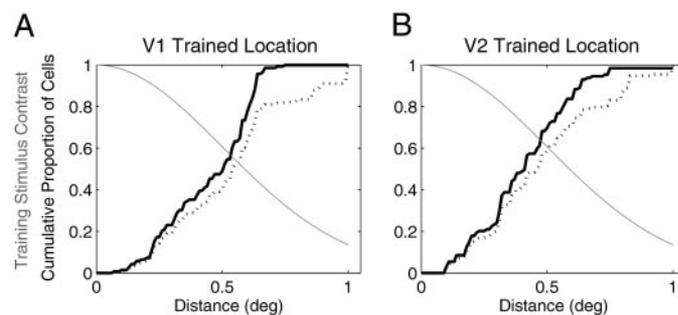

FIG. 2. The distribution of receptive field centers of cells in the trained hemisphere. Gray lines indicate the contrast function of the Gaussian envelope describing the Gabors used for training ($\sigma = 0.5°$). Solid black lines indicate the cumulative distribution of receptive field locations after the application of a 0.75° criterion. The cells described by this distribution were considered to be within the training region for subsequent analyses. Dashed lines indicate the cumulative distribution of distances for all cells recorded from the trained hemisphere.
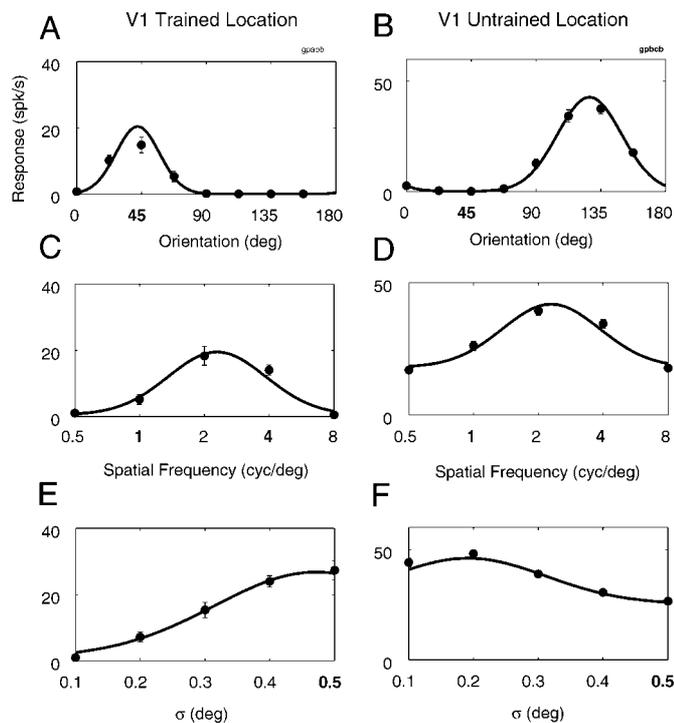
FIG. 3. Two example cells from trained and untrained V1 and their descriptive function fits (solid lines). Circles indicate observed firing rates. Vertical lines indicate ±1 SE error bars, which are too small to be visible in most cases. *A* and *B*: orientation responses and their fitting by a wrapped Gaussian. *C* and *D*: mean firing rates as a function of spatial frequency and their fitting by a Gaussian. *E* and *F*: mean firing rates as a function of stimulus size (σ is the space constant of the Gaussian envelope describing the Gabor patches used as stimuli). Bold values on the abscissas of *A–F* indicate parameter values used during training.

nation training might also affect the response rates of appropriately tuned cells or change the variability of the responses of such cells. Moreover, training effects might be location specific but not orientation specific, or vice versa. To examine these possibilities, all of the parameters of orientation tuning from the fitted cells of the animal-combined populations were examined as a function of preferred orientation and location. Orientation bandwidth, orientation tuning amplitude (peak response minus baseline response), peak response (Fig. 5), and the variance ratio were examined by two types of analyses.

First, correlations between the response parameters and preferred orientation and distance from the center of the training stimuli were examined. For the distance correlations, no distance criterion was used to restrict the populations from either the trained or untrained hemispheres (dashed line, Fig. 2). None of these parameters was correlated with distance from the center of the training stimuli. With one exception, none of these parameters were significantly correlated with preferred orientation either (Hotelling, C-association tests). The exception was a significant correlation between tuning amplitude and preferred orientation in the untrained V1 population (C-association, $P < 0.01$) with cells near the trained orientation having lower tuning amplitudes.

The aforementioned correlation and regression analyses test for relationships between a variety of response properties and the two specific response properties of the training stimuli: orientation and retinotopic location. However, even in the absence of a general relationship between response properties, it is possible that there are differences between neurons that had properties matched to the training stimuli (trained cells) and those that did not (untrained cells). To test for such differences, ANOVA was performed on cells grouped according to their preferred orientation and receptive field location (Fig. 6). Neurons whose preferred orientation was within 22.5° of 45° were classified as belonging to the trained orientation group; while neurons whose receptive field centers were within 0.75° of the training stimuli were classified as belonging to the trained location group. There were no significant effects of location or preferred orientation on orientation bandwidth or peak response in any neuronal population. Tuning amplitude and variance did depend on location, but not orientation, in V1. Tuning amplitude was slightly smaller in the trained population (14.6 spikes/s vs. 19.5 spikes/s), while the difference in variance was more substantial (1.85 vs. 2.36). By contrast, in V2, no orientation-related parameter showed significant dependence on either location or orientation.

Training might have also produced changes in response properties unrelated to orientation. For example, because our training stimuli were of two specific spatial frequencies, the distribution of preferred spatial frequency might be altered for those cells whose preferred orientation was near that of the training stimuli. To examine this possibility, preferred spatial
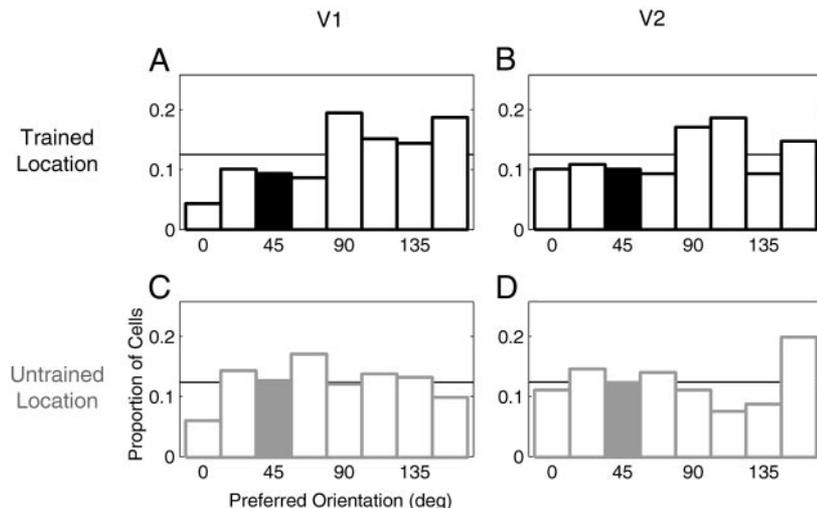

FIG. 4. Preferred orientation distributions for the 4 studied neuronal populations: trained (black) and untrained (gray) representations in V1 (*A* and *C*) and V2 (*B* and *D*). For cells whose orientation responses were well-described by wrapped Gaussian descriptive functions, preferred orientation was defined by the center position of the Gaussian. Data from the 2 animals have been combined. Preferred orientations were then grouped into 8 nonoverlapping bins. The horizontal lines indicate an unbiased distribution in which each bin contains ⅛ of the population. The V1-trained representation has significantly fewer cells at the trained orientation of 45° (filled) than would be expected from an unbiased distribution.
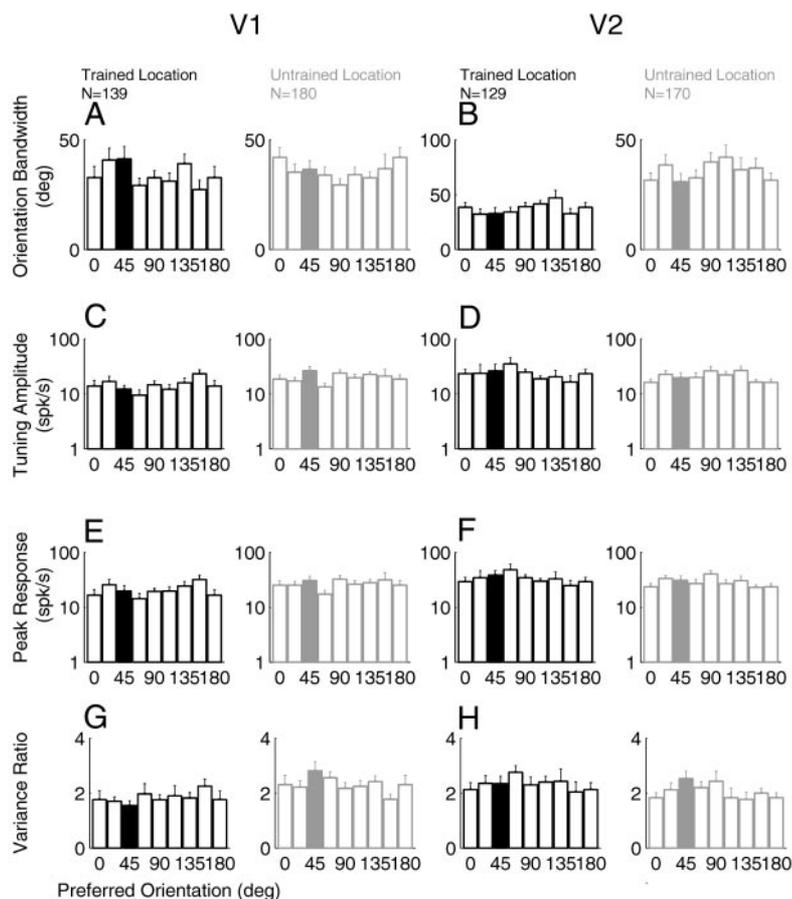
FIG. 5. Receptive field parameters related to orientation tuning obtained by descriptive function fits as a function of preferred orientation for the 4 neuronal populations. Parameters from individual neurons are binned according to location and preferred orientation. Black indicates cells from untrained locations; gray indicates cells from trained locations. Filled bars represent cells whose preferred orientation was within 22.5° of the trained orientation; unfilled bars represent cells with other preferred orientations. For firing rates (C–F) means and variances were computed on log-transformed data. Vertical lines indicate +1 SE for 22.5° width bins. Neither orientation bandwidth (A and B), nor peak response (E and F), nor the variance ratio (G and H) showed any significant variations with either preferred orientation or location in either V1 or V2. However, there was a significant correlation between tuning amplitude and preferred orientation in the untrained V1 population (C-association, $P < 0.01$) with cells near the trained orientation having lower tuning amplitudes.

frequency (Fig. 7, *A* and *B*) and spatial frequency bandwidth (Fig. 7, *C* and *D*), preferred size (Fig. 7, *E* and *F*), and distance from the training stimuli center (Fig. 7, *G* and *H*) were examined as a function of preferred orientation. For preferred size, analyses were done on optimal σ (not shown), as well as optimal σ normalized by eccentricity. No significant correlations between the spatial frequency and size parameters and either preferred orientation or distance from the training stimulus were seen. Furthermore, there were no correlations between preferred orientation and distance from the training stimuli (*G* and *H*).

Few differences were found when cells were grouped according to location and orientation (Fig. 8). By definition, distance varied with location group (*G* and *H*). ANOVAs revealed that peak spatial frequency also varied with location. For preferred spatial frequency, there was an interaction between orientation and location: preferred spatial frequency was relatively low among trained orientation cells in the trained location group (mean = 2.0 cycles/deg), and relatively high among trained orientation cells in the untrained location group (mean = 3.6 cycles/deg).

To summarize, there were few significant changes in receptive field properties associated with the training orientation or location in either V1 or V2. Correlation analysis was done on eight independent receptive field parameters in the four neuronal populations with respect to distance from the training stimuli and preferred orientation. Of these 64 correlation analyses, only 1 was significant: the correlation between tuning amplitude and preferred orientation in the untrained V1 population.

ANOVA for the effects of orientation and location was also done on the eight parameters. In V1, there were location effects on preferred spatial frequency, tuning amplitude, and variance but no effects of orientation alone on any parameter.

The analyses of Figs. 5 and 7 ignore the nonuniform distribution of preferred orientation (Fig. 4) and therefore do not fully characterize the population response to different stimuli. To characterize the combined effects of potential changes in response rates (Fig. 5) and preferred orientation distributions (Fig. 4), we constructed a population response curve for each neuronal population in which the orientation tuning curves from each cell were averaged together (Fig. 9). Such an average takes into account orientation tuning parameters (bandwidth and peak firing rates) as well as the observed distribution of preferred orientation. The population metric therefore indicates the total amount of activity that would be produced by stimuli of different orientations. As expected, none of these population responses show dramatic orientation biases. However, at the trained orientation, the population response was lower in the trained V1 representation than in the untrained V1 representation (Fig. 9*A*). No significant orientation specific differences were seen in V2 (Fig. 9*B*) despite biases in the preferred orientation distribution that are similar to those seen in V1 (Fig. 4). Thus the difference in V1 arises from fewer cells with preferred orientations near that of the training stimuli as well the lower tuning response amplitudes of such cells (Fig. 5*C*).

Because these population response curves are based on individual orientation tuning curves obtained at a variety of
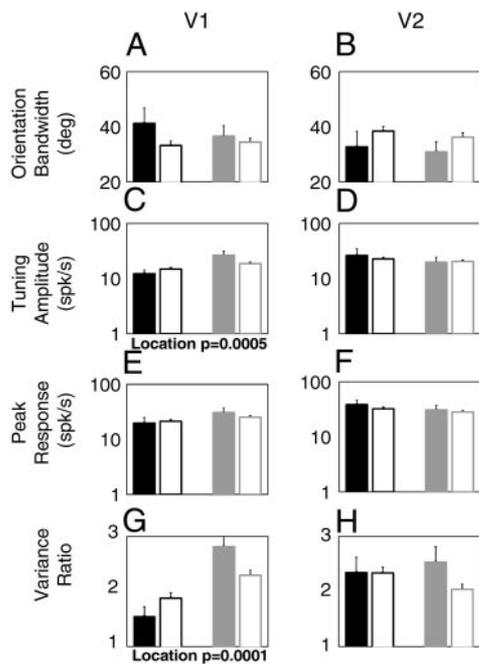
FIG. 6. Receptive field parameters related to orientation tuning grouped according to location and preferred orientation. Color code is the same as Fig. 5. For V1, 139 cells were classified as belonging to the trained location and 180 to the untrained location; for V2, 129 were in the trained location and 170 in the untrained location. For V1, 36 cells had preferred orientations matching the trained orientation, and 283 had unmatched preferred orientations; for V2, 34 were matched, and 265 were unmatched. Consistent with the correlation analyses, most parameters did not depend on orientation or location.

different spatial frequencies, significant orientation biases might exist among the subset of cells preferentially tuned to the spatial frequencies used in training (1 and 4 cycles/deg). To estimate the orientation population response at these spatial frequencies, we made use of the separability between orientation and spatial frequency (Webster and De Valois 1985), and for each cell constructed a orientation-spatial frequency response surface by multiplying the appropriately normalized tuning curves together for cells whose orientation and spatial frequency responses were well fit by descriptive functions (Fig. 9, *C* and *D*). Again, there are no large variances in population response as a function of orientation. Indeed, at a spatial frequency of 1 cycles/deg, there is no significant difference in orientation bias between the trained and untrained V1 populations. However, the orientation bias seen in the mixed spatial frequency average (*A*) is visible at a spatial frequency of 4 cycles/deg: responses at the trained orientation are lower in the trained population than in the untrained population (*C*). This indicates that the observed effects on the neuronal response properties would primarily effect the responses to the training stimuli with higher spatial frequencies.

Retinotopy

For both animals, visuotopic mapping was measured in the trained and untrained hemispheres by relating the position of each V1 penetration to the average of observed receptive field locations within that penetration. This method has limited accuracy because electrodes were secured several centimeters above the cortical surface, were not perfectly normal to the cortical surface, and were typically remounted and replaced on

a daily basis. In *monkey 2,* visuotopy in and around the training region was also measured in an acute recording session for both V1 and V2.

Linear magnification factors were computed by dividing the penetration distance by the visuotopic distance for all possible pairs of penetrations. To evaluate the dependence of magnification on eccentricity, regression analysis was applied to the magnification factors as a function of the average eccentricity of the penetration pair (Fig. 10, *A* and *B*). For all cases except the V2 data from the second animal (Fig. 10*B*), there was a significant negative correlation between magnification and eccentricity. Each magnification factor was then normalized according to the magnification factor predicted by the regression equation (Fig. 10, *C* and *D*), and these normalized factors were plotted as a function of distance from the center of trained region. Correlation analysis revealed that in none of the acute or chronic recording (not shown) data sets was there a significant non-zero correlation between eccentricity corrected magnification and distance from the training region. Thus our training produced no measurable effect on the visuotopic mapping in either V1 or V2.

Neurometric performance

Although the slight reduction in the trained V1 population response at the trained orientation appears inconsistent with orientation-specific improvement in performance, it might be the signature of response property changes that support improved performance. An orientation-selective cell is maximally sensitive to changes in orientation not at its preferred orientation (Fig. 11, *A* and *B*), but rather at orientations displaced from the peak of the curve (Fig. 11, *C* and *D*), where the slope of the orientation response function is the greatest. If a relative excess of neurons preferred orientations offset from the trained orientation, the population response to the trained orientation (Fig. 9) would be reduced. However, the population response shown in Fig. 9 is only a partial description of how neurons contribute to discrimination because it ignores the variance of neuronal responses and their spatial frequency tuning. For example, responses in the trained V1 population were less variable than those of the untrained V1 population (Fig. 5*G*). This should improve the discriminability of signals from the trained location. Additionally, because the average preferred spatial frequency was lower among V1 cells in the trained orientation and location groups (Fig. 8*A*), discriminability should be improved by the relatively large responses to the 1 cycle/deg stimuli.

A behaviorally relevant description of the neuronal population must incorporate both the mean and variances of the responses of individual neurons to the stimuli used in the behavioral measurements (Table 1). Using such a description, we wish to ask three questions. First, how does behavioral performance compare with the performance of an ideal observer of individual neuronal responses? Second, how does behavioral performance compare with an observer of a population of neurons? Third, can patterns in the behavioral data be used to rule out or implicate specific decision and pooling models? All of these questions depend on invoking specific models of how physiological responses are used to make behavioral decisions. These models must specify the signals that are used for the decision (responses to particular orienta-
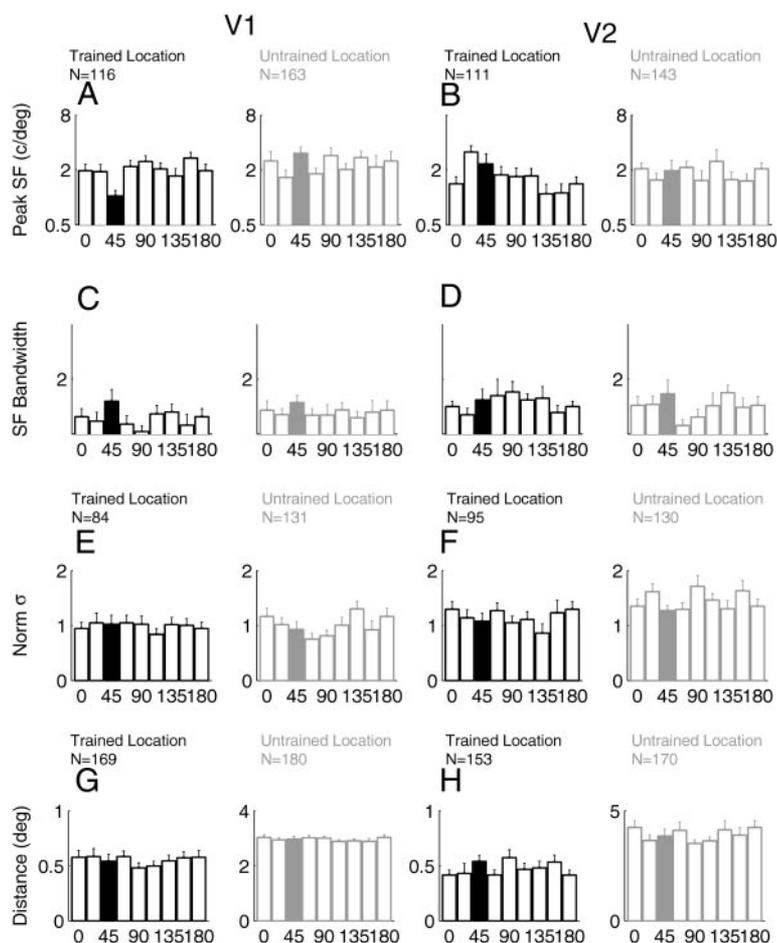
FIG. 7. Receptive field parameters not related to orientation tuning as a function of preferred orientation for the 4 neuronal populations. Format is the same as Fig. 5. Neither spatial frequency bandwidth (*C* and *D*) nor preferred size (*E* and *F*) depend on preferred orientation or location. By definition, the distance from the training center was different between the trained and untrained representations irrespective of preferred orientation (*G* and *H*). However, preferred orientation and distance from the training center were independent for each population.

tions in our case), the method by which signals are compared (decision model), and how signals from multiple neurons are combined (pooling).

The decision model that has been traditionally applied to neuronal response data is a discrimination model. In this model an observed response is assigned to one of two response distributions. The reliability of such an assignment depends on the separation between the two response distributions: for largely overlapping distributions, there is little chance of a correct assignment (Fig. 11*A*); whereas for widely separated distributions, such assignments should be very accurate (Fig. 11*C*). In our case, the response distributions to orientations 3° away from 45° are compared to the response distribution of 45° stimuli (Fig. 11*A*). An alternative to the discrimination model is the classification model, in which an observed response is assigned to an orientation range (Fig. 11, *B* and *D*) on the basis of responses over the entire range. For both of these decision models, response means and variances were computed using the fitted descriptive functions for orientation and spatial frequency. To infer responses for arbitrary stimuli, we used the complete orientation-spatial frequency response surface for each cell obtained by multiplying appropriately normalized orientation and spatial frequency descriptive functions under the assumption of separability (Webster and De Valois 1985).

In any of these models, performance improves as the pool size is increased, and degrades with the introduction of noise or correlation between the neurons. To compare different decision and pooling models (see APPENDIX), we computed performance for a variety of pool sizes and estimated by linear interpolation the number of neurons necessary to achieve behavioral levels of performance at the trained orientation in the absence of noise or interneuronal correlations. We used this number as a summary statistic of the suitability of the four neuronal populations and five decision/pooling models to the discrimination task. A neuronal population that achieves a given behavioral performance with a smaller pool size than other populations is better suited to the behavior task. For every model and population, we computed performance on 6° orientation changes around 45°, and around 135°.

Figure 12 shows d' performance as a function of pool size in all four neuronal populations when discrimination-based response pooling is invoked. Solid horizontal lines indicate behavioral performance: 80% correct ($d' = 1.2$) at the trained orientation (*A* and *C*), and 50% correct (chance, $d' = 0$) at the untrained orientation (*B* and *D*). Individual cells (pool size = 1) of both trained (black) and untrained (gray) populations were much worse at discrimination at the trained orientation than the animal subjects. Thus, in contrast to most previous studies, even the best cells that we observed would be unable to provide a basis for the monkeys' behavior. Consistent with the behavioral observations, there is little difference between V1 and V2 at the two locations: signals from the individual neurons of both populations are similarly incapable of supporting discrimination decisions. However, the suitability of the neuronal populations is inconsistent with the behavior: in both V1 and V2 the untrained populations (gray) are capable of
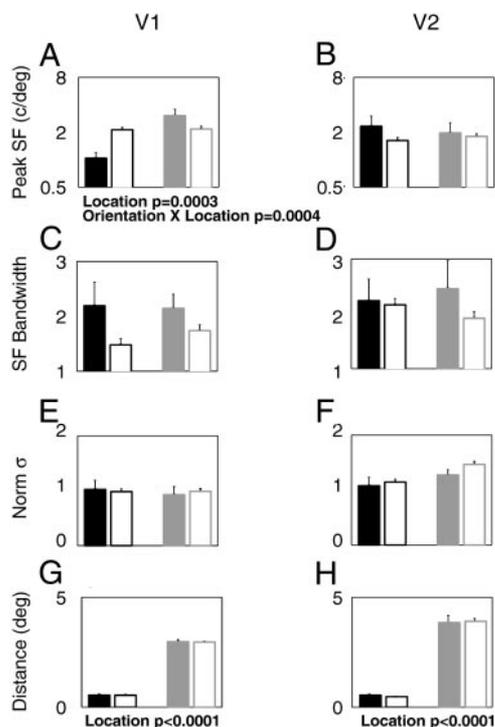
FIG. 8. Receptive field parameters not related to orientation tuning grouped according to location and preferred orientation. Format is the same as Fig. 6. Only cells whose spatial frequency responses were well fit by descriptive functions are included in *A–D*. For these panels, 116 V1 and 111 V2 cells were in the trained location, and 163 V1 and 143 V2 cells were in the untrained location. With respect to the trained orientation, 29 V1 cells and 29 V2 cells had matched preferred orientation, and 250 V1 and 225 V2 cells had unmatched preferred orientations. There was a significant effect of location on peak spatial frequency, as well as an interaction between orientation and location in V1 (*A*). Only cells whose sigma responses were well fit were included in *E* and *F*. For these panels, 84 V1 and 95 V2 cells were in the trained location, and 131 V1 and 130 V2 cells were in the untrained location. With respect to the trained orientation, 26 V1 cells and 29 V2 cells had matched preferred orientation, and 189 V1 and 195 V2 cells had unmatched preferred orientations. In *G* and *H,* all cells recorded in the trained hemisphere were included irrespective of receptive field position relative to the training stimuli. For these panels, 169 V1 and 153 V2 cells were in the trained location, and 180 V1 and 170 V2 cells were in the untrained location. With respect to the trained orientation, 38 V1 cells and 38 V2 cells had matched preferred orientation, and 311 V1 and 285 V2 cells had unmatched preferred orientations. As dictated by the grouping, there is a significant effect of location. However, receptive field position does not depend on preferred orientation.

providing better performance than the trained populations (black). Finally, for both the trained and untrained populations, V2 surpasses V1 in performance. Thus, of the four neuronal populations, untrained V2 was the best suited for the trained task, while trained V1 was the most ill-suited. Thus the weaker population response of trained V1 is not consistent with an increased ability to discriminate changes in orientation.

To test this specific pooling and decision model, we also computed performance as a function of pool size for 6° discriminations around an untrained orientation (Fig. 12*B*). The pool sizes obtained from Fig. 12*A* were used to predict performance on this task. Since the animals could not perform such a task, the behavioral *d′* is zero. The predicted *d′* is computed by using the pool size necessary to explain performance at the trained orientation. These predicted *d′*s are all much larger than the behaviorally observed value of zero. Despite the behavioral difference between trained and untrained orientations, the per-

formance of these models for all neuronal populations and pool sizes is similar to that seen with the trained orientation. Indeed, in some cases, the pooled ideal observer performances are actually better in the untrained orientation (*B*) than in the trained orientation (*A*).

The physiological properties of the observed populations therefore do not reflect the orientation selectivity of the psychophysical observations. However, most cells are ill-suited for discrimination around the trained orientation: the majority of neurons have a *d′* near zero. Consistent with previous neuronal pooling models (Britten et al. 1992; Prince et al. 2000; Shadlen et al. 1996), we have included both neurons that are well suited for the discrimination by virtue of their tuning properties as well as those that are not. Ideal detector performance can be significantly improved at a particular orientation by introducing a pooling bias, so that only those cells that are most capable are considered. This is equivalent to stating that, although our sampling was unbiased with respect to all cells, the sampling the animal used to arrive at decisions was biased. Such a bias will also have the effect of worsening performance at other orientations. In our case, an "optimized" pool will be one in which only cells whose peak orientation is near the trained orientation are considered: this will increase performance at the trained orientation and decrease performance at the untrained orientation.

We implemented this optimized pool for each neuronal population by shifting each neuron's orientation tuning function while keeping all other parameters (response rate, spatial frequency tuning, and variance) fixed. For each neuron, the peak orientation was displaced from the trained orientation such that the maximum slope of the orientation tuning function was aligned with the trained orientation (Fig. 11, *C* and *D*). Figure 12, *E–H,* indicates the performance of these optimized populations at both the trained and untrained orientations for discrimination-based decisions. Even with this optimized population, individual neurons (pool size = 1) are incapable of providing a discriminable signal sufficient to explain behavior (*E* and *F*). However, the average discriminability performance of single neurons is sufficiently changed so that the pooled performances are now highly dependent on orientation: for the same pool size the performances of the orientation-biased discrimination pools (*E* and *F*) are much better at the trained orientation than at the untrained orientation (*G* and *H*). Although only the results of a response pooling model are shown in Fig. 12, the conclusions from a decision pooling model (see APPENDIX) are identical: trained V1 is the least suited to the perceptual task, and an orientation-biased pooling is necessary to replicate the orientation dependence of the behavior.

Figure 13 shows the results for models in which decisions are reached by pooling the stimulus classification decisions from individual neurons. As with the discrimination models, each neuronal population was considered separately for trained and untrained orientations, and performances were evaluated as a function of neuronal pool size. Just as with discrimination, individual neurons are poor at classification with most neurons performing at near chance level. As with discrimination, under the classification models the trained and untrained neuronal populations are similar to one another, and the V2 populations are better than the V1 populations. Similarly, there is a lack of orientation bias in the observed populations (Fig. 13, *A* and *B*
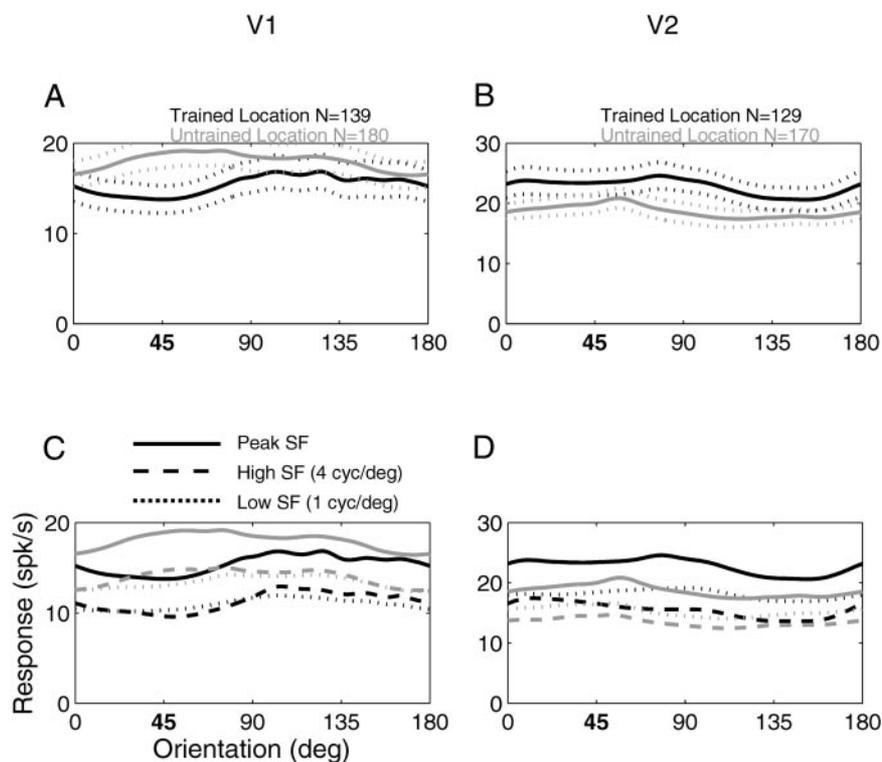
FIG. 9. Average responses in the 4 neuronal populations as a function of orientation. Solid line indicate means; dashed lines, SEs. The combined effect of the paucity of cells whose preferred orientation was near the trained orientation (bold; Fig. 4), and the lower tuning amplitude of such cells (Fig. 5) creates a dip in the population response in the trained V1 representation at the trained location (*A*). No such dip is visible in V2 (*B*). *A* and *B*: orientation tuning averages based on the peak spatial frequency for each cell. *C* and *D*: the expected mean population response to stimuli at the 2 spatial frequencies used in training. The dip at the trained orientation in the V1 trained population is only visible for high spatial frequency stimuli (thick dashed line).

vs. *C* and *D*), so that the predicted performance with unbiased pooling (dashed lines, *B*) at the untrained orientation exceeds behavioral observations (solid line, *B*). By shifting orientation tuning functions (Fig. 11*D*), we constructed populations (Fig. 13, *E* and *F*) that solely contained cells whose orientation tuning was optimized for classification. As with discrimination, this produced the expected orientation bias: an increase in performance at the trained orientation (*E* and *F* vs. *A* and *B*) and a decrease in performance at untrained orientations (*G* and *H* vs. *C* and *D*) among individual neurons and the populations as a whole. The results for task-based detector pooling (see APPENDIX) also exhibited these patterns.

Thus, although both discrimination and classification models applied to individual neurons are unable to explain behavioral performance, models in which signals from the most appropriate neurons are combined can explain orientation-dependent discrimination performance. In the absence of large orientation biases in either V1 or V2 representations of trained and untrained locations, orientation-selective (and location invariant) pooling must be invoked to explain the behavior. However, the predicted performance of orientation-biased models for the untrained orientation still exceeds behavioral observations (Figs. 12 and 13*D*).

This suggests that, even with orientation-biased pooling, our models might not be able to account for the full pattern of behavioral performances observed around different orientations and with different changes in orientation. This pattern was measured in *monkey 2* using probe trials randomly inserted into the standard protocol in which stimuli are oriented near the trained orientation of 45° and is shown in Fig. 14*A*. The most notable feature of the behavioral performance surface is that high performance is limited to orientations near the trained orientation even when the difference between nonmatching stimuli is between 20 and 30°, which is the naive discrimination threshold (Fig. 1).

Because such large changes should be easily discriminable independent of orientation, this suggests that the animal is not using a discrimination algorithm to arrive at match/nonmatch decisions.

To compare these behavioral data with our decision and pooling models, we used the optimized discrimination and classification pools and tested performance over a matching range of orientations and orientation changes (Fig. 14). For each model we constructed a pool of 100 neurons whose orientation tuning was optimized for the trained orientation. Model performances were then normalized (i.e., noise was incorporated) so that 79% correct performance was obtained at 45° with an orientation change of 6°. As indicated by *C* and *D* in Figs. 12 and 13, with the addition of orientation-selective pooling, all of the models considered so far are able to produce much better performance at the trained orientation than at an orthogonal orientation with orientation changes of 6°. However, the models shown in Figs. 12 and 13 predict little orientation selectivity once the nonmatch difference exceeds 20° (*B* and *C*). Thus a different pooling model is required to replicate the behavioral data. One such model is a classification model in which responses are pooled (*D*) prior to stimulus classification. This essentially reduces the neuronal pool size to a few "super-neurons" which receive inputs from a large number of optimized V1 and V2 neurons. The large difference between the models of Figs. 12 and 13, and this classification model can be easily illustrated by considering a particular point on the behavioral surface of Fig. 14: for example a 30° change around 90°. For a discrimination model, this is hardly a challenge since even with orientation biases in the pool there are sufficient neurons with response differences over this 30° range to ensure good performance. For the response pooled classification model, in which decisions are solely based on high-low orientation classifications of a small number of "super-neurons," performance is poor be-
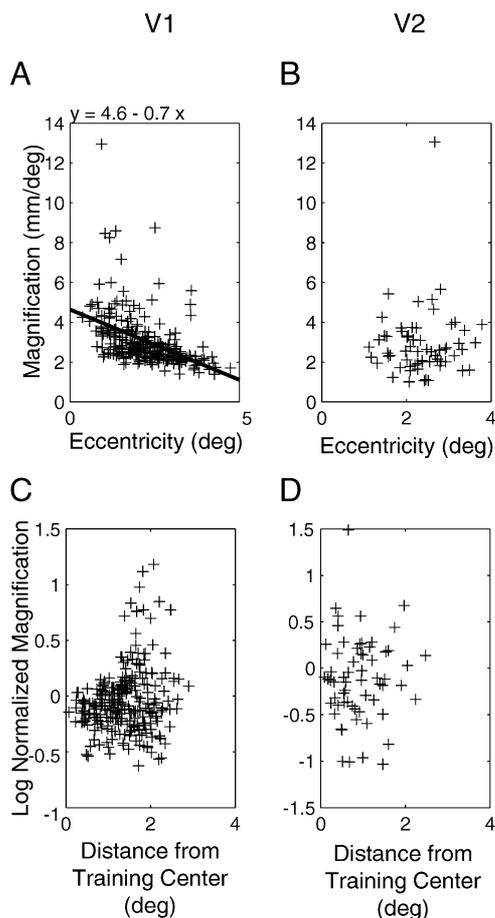
FIG. 10. Magnification factors in the trained and untrained V1 (*A* and *C*) and V2 (*B* and *D*) representations. *A* and *B* indicate magnification factors as a function of eccentricity; *C* and *D* indicate magnification factors normalized according to the regression prediction of the *left panel*. With the exception of the V2 population (*B*), all populations showed a significant negative correlation between magnification and eccentricity. However, when the eccentricity effects are compensated for by the normalization procedure, there is no correlation between magnification and distance from the center of the training region (*C* and *D*). Thus, other than the expected change in magnification with eccentricity, there were no significant changes in visuotopy as a function of position in visual space in either the trained or untrained representations.

cause both of the orientations presented in a nonmatch trial would be labeled as "high," i.e., above 45°.

DISCUSSION

We have studied perceptual learning by recording individual neurons in early cortical visual areas of monkeys trained in an orientation discrimination task at a specific retinal location and centered around a specific orientation. After extensive training, the animals' improved performance was orientation specific, but not highly dependent on location. Thus the dependencies of the perceptual learning observed were not completely consistent with the training stimuli. None of the receptive field parameters examined (orientation bandwidth, peak response, tuning amplitude, variance, preferred spatial frequency, spatial frequency bandwidth, and preferred size) was substantially affected by the training, and almost none of the small changes was statistically significant. In the only case in which there were effects of orientation (tuning amplitude), there was also

an interaction between location and orientation. A similar pattern is seen in the population response curves that indicate a small orientation- and location-specific reduction in response (Fig. 9). These small changes might be explained by the effects of repeated presentation and are not well correlated with the largely location invariant behavioral effects of our training.

Consistent with this suggestion, the responses of the individual recorded neurons are incapable of producing the behavioral observed levels of performance. Instead, individual neurons must be pooled before decision making. Moreover, the pooling itself must be orientation selective in order for such an orientation unbiased population to account for orientation-specific improvements in discrimination. Finally, the performance of various pooling models across a range of orientation discrimination tasks suggests that decisions in the trained animals relied on stimulus classification rather than stimulus discrimination.

Training-related improvement in visual tasks

Improvement in visual performance with practice has been reported in a wide variety of visual tasks including stereoacuity (Fendick and Westheimer 1983; O'Toole and Kersten 1992; Ramachandran 1976; Ramachandran and Braddick 1973), vernier acuity (Beard et al. 1995; Crist et al. 1997; Fahle and Edelman 1993; Fahle et al. 1995; McKee and Westheimer 1978; Saarinen and Levi 1995), search (Ahissar and Hochstein
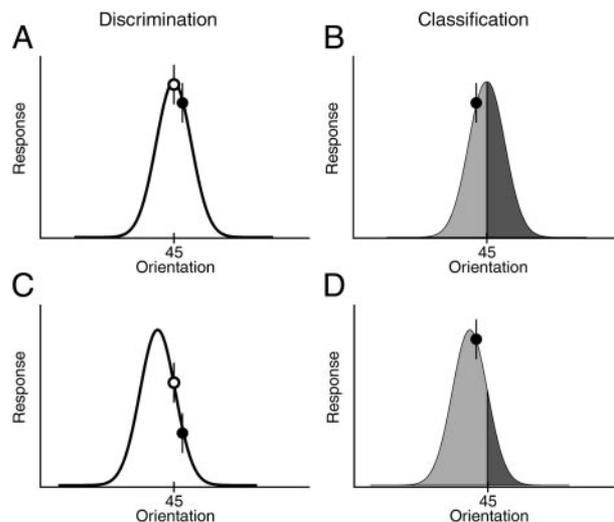

FIG. 11. Discrimination and classification decision models applied to individual neuronal responses. In the discrimination model, orientations are evaluated by comparing an observed response (filled circle) to a template response (open circle) at the trained orientation (45°). In the classification model, orientations are evaluated by comparing the likelihood that the observed response is a response to an orientation less than 45° (gray region) to the likelihood that the response is a response to an orientation greater than 45° (black region). For both models, neurons whose peak orientation is at 45° provide poor signals for making an orientation decision. For the discrimination case (*A*) a small shift in orientation around the peak is associated with a small change in response. For the classification case (*B*), the observed response is equally likely to have originated from an orientation less than 45° as from an orientation greater than 45°. In both models neurons whose optimal orientation is not 45° can provide better performance. In the discrimination model (*C*), the small shift between observed and template responses is now associated with a larger change in response. In the classification model (*D*), the observed response will be associated with an orientation less than 45° (gray region) since no orientation in the black region produces such a response.
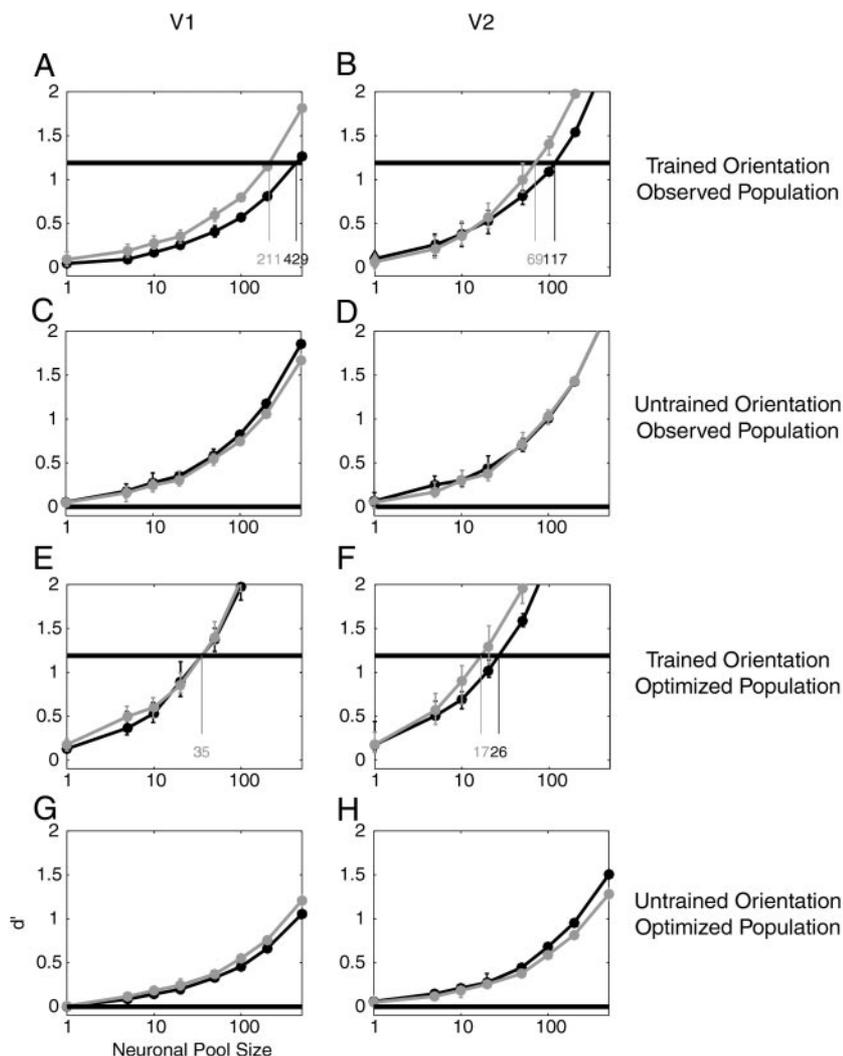
FIG. 12. Ideal observer performance as a function of neuronal pool size for the 4 neuronal populations with discrimination-based decisions. Circles represent median performance for a pool size; error bars, the top and bottom quartiles of the performance distribution for a given pool size. Orientation differences of 6°, for which performance is around 79% at the trained orientation were used. Solid horizontal lines correspond with the d' associated with 79% (trained orientation, *A, B, E,* and *F*) and 50% (untrained orientation *C, D, G,* and *H*) performance in a 2-alternative forced choice. In all cases individual neurons are considerably worse than the animals' performance at the trained orientation. Consistent with psychophysical observations, performances are approximately consistent between trained (black) and untrained (gray) representations for both V1 (*A*) and V2 (*B*). However, inconsistent with behavioral observations, performance is not orientation dependent: it is similar at an untrained orientation orthogonal to the trained orientation (*C* vs. *A, D* vs. *B*). Thus the predicted performance at the untrained orientation using the pool sizes necessary for performance at the trained orientation far exceeds behavioral observations. Orientation dependency can be introduced by assuming a biased sampling so that decision pools only include the most capable neurons (*E–H*). With such biased pooling, the performance curves for the trained orientation shift leftward (*E* vs. *A, F* vs. *B*), and performance curves for the untrained orientation shift rightward (*G* vs. *C, H* vs. *D*). A smaller number of neurons is required to explain the behavior at the trained orientation (*E* vs. *A, F* vs. *B*), and predicted performance at the untrained orientation is much closer to the chance levels seen in behavior (*G* and *H*).

1997, 2000; Ellison and Walsh 1998; Fiorentini 1989; Karni and Sagi 1991, 1993; Schoups and Orban 1996; Sigman and Gilbert 2000; Sireteanu and Rettenbach 1995, 2000), object identification (Furmanski and Engel 2000), and discrimination of differences in direction (Ball and Sekuler 1987; Zohary et al. 1994), orientation (Matthews et al. 1999, 2001; Mayer 1983; Schoups et al. 1995b; Vogels and Orban 1985, 1994a), spatial frequency (Fine and Jacobs 2000), and spatial phase (Berardi and Fiorentini 1987; Fiorentini and Berardi 1980, 1981). The range of techniques, time courses, and measures of these learning effects makes comparison difficult (I. Fine and R. Jacobs, personal communication). However, one common theme in many of these experiments is that the learning shows specificities that are suggestive of the involvement of early levels of visual processing. For example, training-related improvements in stereoacuity with random-dot stereograms are specific for both location and orientation (Ramachandran 1976; Ramachandran and Braddick 1973). Thus it is tempting to conclude that the site of neuronal plasticity associated with such specific improvements is in the early visual areas where orientation-selective cells with small receptive fields are common. The location and orientation specificity of many psychophysical studies has led to the suggestion that physiological changes in early visual areas are associated with some perceptual learning tasks. However, there are several alternative explanations for such specificity: cells in higher visual areas that are particularly sensitive to position and orientation might be involved, or the pooling of signals from V1, due to selective attention, for example, might change without any change at the level of V1 itself.

In this regard it is notable that the perceptual improvements in this study do not show many of the specificities reported in other demonstrations of perceptual learning. Moreover, the perceptual improvements do not reflect the specificities of the training. For example, the performance of *monkey 2* varied little across different spatial frequencies, although only two spatial frequencies were used during training. This is in contrast to spatial frequency specificity reported in training humans for spatial phase discrimination (Fiorentini and Berardi 1980, 1981). Even more striking is the comparison of our data to the location specificity found in psychophysical studies of improvements in orientation discrimination with training. Human studies have shown improvements that not only fail to transfer across hemifields (Shiu and Pashler 1992), but also fail to transfer even to adjacent regions of visual space (Schoups et al. 1995b). A recent study reported quadrant-specific training effects in monkeys trained in an orientation- and location-specific manner (Schoups et al. 2001). In contrast, in both of
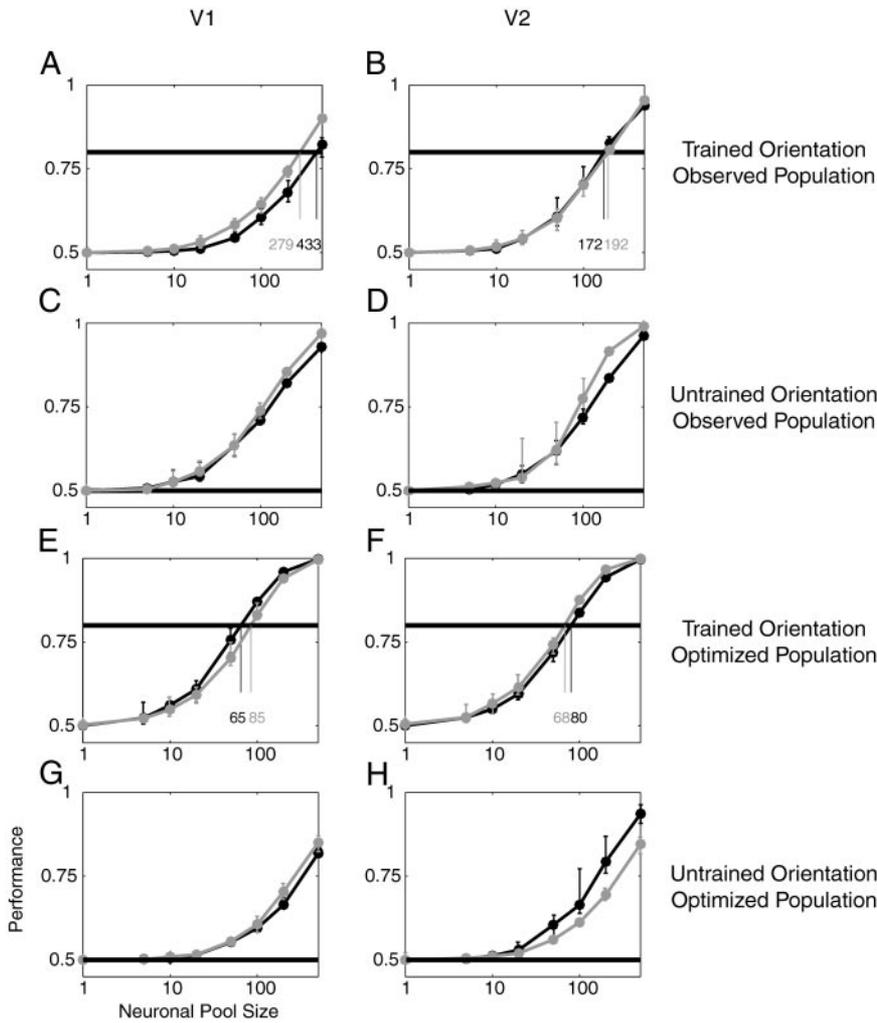
FIG. 13. Ideal observer performance as a function of neuronal pool size for the 4 neuronal populations with classification-based decisions. Format is the same as Fig. 12. As with the discrimination models, individual cells are much worse than the animals' behavior, and there are not large differences in either V1 or V2 with location (black vs. gray) or orientation (*A* vs. *C, B* vs. *D*). As with Fig. 12, selective pooling draws from a group of neurons with optimal orientation tuning for classifying orientations around 45° and creates a orientation dependency (*E* vs. *G, F* vs. *H*) in performance across all pool sizes.

our monkeys, performance was similar in the hemifield opposite to the training (Table 1). Although there are many plausible explanations for the difference between our results and those of human studies, the methodological differences between our study and the recent monkey study are more subtle: both of these studies involved training monkeys in an orientation discrimination task using stimuli that did not contain consistent positional clues over a period of several months. While the exact cause of the positional insensitivity that we observe remains to be established, the difference between our

results and those of other studies suggests that position selectivity of perceptual improvements is sensitive to small changes in task design. For example, transfer of learning improvements in human spatial phase discrimination across visual hemifields is dependent on spatial frequency and distance from, and symmetry with respect to, the vertical meridian (Berardi and Fiorentini 1987). It is also possible that the introduction of a distracting feature (spatial frequency) in our training, in addition to increasing task difficulty, may encourage generalization for attributes other than orientation such as location. In any
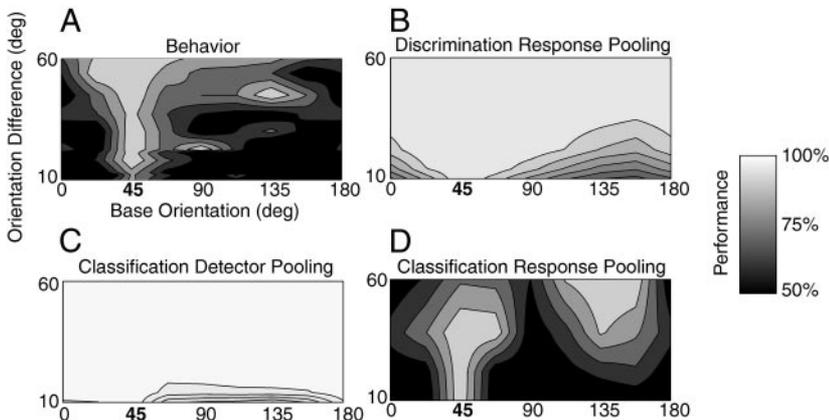

FIG. 14. Performance as a function of base orientation and orientation change in nonmatching trials. Black indicates chance performance, and white indicates 100% correct. Observations of *monkey 2*'s performance in probe trials indicate that discrimination performance is poor for base orientations different from the trained orientation, even when the orientation change is large (*A*). The discrimination-based model of Fig. 12*B* and the classification based model of Fig. 13*C,* on the other hand, indicate that even for a pool of neurons specifically chosen for discrimination at 45°, performance should be excellent for orientation changes larger than 25°, irrespective of the base orientation. Only a classification model in which responses are pooled to arrive at stimulus classification decisions (*D*) is able to produce such poor performance for base orientations other than the trained orientation.

case, the relative insensitivity of our results with respect to location suggests the involvement of either a network of long-range connections or neurons with very large receptive fields. Since the only neurons in early visual areas that have ipsilateral excitatory regions are within a degree of the vertical meridian, such large receptive fields could only be found in higher visual areas.

In some respects our results are consistent with previous studies of discrimination training. For example, behavioral improvements in humans trained in a line bisection task at a specific orientation and location were much more orientation specific than location specific: improved performance was seen 8° away in a different quandrant from the trained location (Crist et al. 1997). Consistent with human studies of orientation discrimination training, we found that improvements in discrimination were limited to orientations near the trained orientation. Moreover, our physiological observation of a slight orientation specific reduction in response after discrimination training has also been found in both monkeys (Schoups et al. 1997) and humans (Schiltz et al. 1999). These observations are consistent with the effects of adaptation, in which responses are reduced with repeated presentations. Indeed, orientation-specific adaptation has been observed behaviorally in humans (Matthews et al. 2001; Regan and Beverley 1985). However, there are number of reasons to rule out the orientation-specific response suppression as being simple adaptation. First, although training stimuli were presented at the beginning of each training session in order to verify behavioral thresholds, when we searched for cells we did so by presenting stimuli at all orientations. Because adaptation is typically described with a time constant on the order of seconds, the initial training would be unlikely to affect our measurements of orientation selectivity. Second, if repeated presentations necessarily reduce responses, then dips would also appear in the population spatial frequency response curves at the two spatial frequencies used in the training. No such differences were seen in the population spatial frequency responses of trained and untrained locations. There is also behavioral evidence distinguishing training and adaptation: orientation discrimination training increases contrast sensitivity, while orientation adaptation decreases contrast sensitivity (Matthews et al. 2001).

It is also possible that because we studied neurons during a foveal discrimination task we were inadequately characterizing neuronal responses during the actual performance of the task. We examined receptive field properties when monkeys were not doing the trained task for several reasons. We wished to avoid distorting responses with modulation related to nonspecific arousal when the training stimuli, which had been presented for many months, appeared. Such distortions might selectively increase responses to the trained orientation without any fundamental change in receptive field properties. Because previous demonstrations of receptive field changes associated with long-term training were measured in anesthetized preparations where attentive and motivation considerations are uncontrolled, such distortions would also complicate comparisons to previous studies. To study every neuron encountered in an unbiased manner, we would have to present task stimuli that were not orientation and spatial frequency specific and therefore might interfere with the training. This problem could be avoided by only presenting stimuli that were presented during training but then, given the majority of neurons do not respond

to such stimuli, we would not have fairly characterized the neuronal population. Finally, large task effects have not been reported in V1, and even if they existed, would probably not alter fundamental receptive field properties such as orientation bandwidth and response variability (McAdams and Maunsell 1999a,b).

Our results are largely consistent with two reports in which V1 neurons were studied after prolonged visual training. Using a design much like the one described here, Schoups and colleagues trained monkeys to discriminate the orientation of gratings that were presented at a consistent location and around a specific orientation (Schoups et al. 1997, 2001). As with our results, they reported a slight decrease in the population response to the trained orientation in the trained population (Schoups et al. 1997). However, they found no shift in the distribution of preferred orientations (Schoups et al. 2001). They described an orientation-specific increase in the average absolute value of the slope of normalized orientation tuning functions at the trained orientation for neurons whose optimal orientation was near the trained orientation. This effect was limited to neurons whose optimal orientations were between 12 and 20° from the trained orientation. Although they did not explicitly compute bandwidth, this suggests that bandwidths near the trained orientation changed, which was not seen in our data (Fig. 5A). To compare our data directly, we computed average slopes using normalized orientation tuning functions for neurons whose optimal orientation was within 12 and 20° of the trained orientation, and for neurons whose optimal orientation was within 12 and 20° of the orientation orthogonal to the training stimuli. Analysis of the four groups of cells (trained and orthogonal orientations at trained and untrained locations; ANOVA) revealed no significant effects. To examine peak slope as a function of orientation, we also plotted peak slope versus the orientation at which this peak occurred for all cells. Although the results from Schoups and colleagues suggest that this average peak slope would be larger near the trained orientation, no such effect was present in our data: average peak slope did not vary with orientation (Hotelling), nor were there effects of orientation or location when cells were grouped (ANOVA).

It is possible that the larger sample size (1,430 vs. 449 V1 cells) enabled them to see small differences that are not apparent in our study. Given the difference in the psychophysical results, we feel that the most likely explanation for any differences lies in the nature of the trained task. However, it is not clear that there is a substantial discrepancy between our study and Schoups et al. (2001). For example, it is unclear how the slope changes reported by Schoups et al. (2001) relate to the classically described receptive field properties, such as tuning bandwidth, responsiveness, and size, that have been well-established for V1 cells and studied in other sensory cortices. Our data indicate that these classical measures are largely unchanged with training. Additionally, because normalized response functions exaggerate the influence of weakly responding cells on the population response, the described slope changes might have little effect on the population response. Finally, because these slope changes do not incorporate responsiveness or response variability, it is not clear how to relate them to classic models of signal detection theory, such as the d' discriminability measure.

In the second report, V1 neurons were studied in monkeys

that were trained in a line bisection task for many months (Crist et al. 2001). Although it is uncertain how specific the behavioral improvements were after such training, the time course of improvement is similar to what we have reported. Additionally, although receptive field properties were not extensively examined, those properties that were examined (retinotopy and orientation bandwidth) showed no significant change. Crist et al. reported that surround interactions were different for neurons within the training region. However, because interactions studied while the task was being performed were compared with interactions when the monkey was simply fixating, it is unclear whether the difference reported is due to stimulus and/or task differences or some change in receptive field properties. Moreover, even if surround interactions were altered, because these interactions involve stimuli outside of the training region, they could not directly subserve the perceptual improvements seen as a consequence of training.

This is consistent with our data suggesting small changes at the level of V1 that arise as a consequence of training but which are not directly responsible for the behavioral improvement. For example, we saw small orientation- and location-specific effects consistent with orientation and location specificity of the training stimuli but not consistent with the final trained behavior (Table 1). The possibility that different areas can be involved in the task before and after training is supported by human experiments in which transcranial magnetic stimulation selectively disrupted novel, but not learned, visual searches (Walsh et al. 1998) and had diminished effects with repetition of a letter identification task (Corthout et al. 2000). However, since our behavioral measurements show orientation-specific but location-unspecific changes *after* learning, and since orientation-selective cells can be found in many visual areas including areas whose cells have large receptive fields, our behavioral data are not strongly suggestive of a central role for the early visual areas in the trained animal. Moreover, the discrepancy between the large orientation-specific behavioral changes and relative mild orientation-specific changes in the V1 population responses also suggests that the neurons subserving the behavioral improvement are not located in V1 or V2.

Plasticity in other sensory systems

In auditory and somatosensory cortex, training has been shown to change both the topographic organization and the distribution of response selectivities among individual neurons. To compare data from different studies, we computed the ratio of cortical area devoted to the training task before and after training, as well as the ratio of receptive field size within this cortical region before and after training. To see the degree of subject variability, all ratios were computed separately for each animal in each of the studies. Because our training involved two specificities that are mapped on the cortical surface, namely location and orientation, there are two potentially independent remappings that may occur. To examine changes in visuotopy, we compared the ratio of the magnification factors in the trained and untrained representation. To examine changes on the receptive field level for visual space, we compared average receptive field sizes, as characterized by the optimal size, for cells in the two representations.

Figure 15 compares our results to the changes seen in auditory and somatosensory cortex. In this figure, distance from the origin corresponds to the amount of change associated with training. While there is little intersubject variation within any single study, there is little consistency between the different studies. For example, neither of our animals showed changes in either visual space topography or receptive field size (black triangles), while one study of somatosensory area 3b (Recanzone et al. 1992b) found large increases in both magnification and receptive field size associated with frequency discrimination training among all their animals. The angular position of points in Fig. 15 indicates the relative change of topography and other receptive field selectivities. The product of the magnification factor (mm/deg) and receptive field size (deg) is the point image: the cortical area corresponding to the representation of an average receptive field. Because the point image (mm) in primary cortex does not vary greatly with eccentricity (Hubel and Wiesel 1974) and is similar between different sensory cortical areas (Sur et al. 1980), it is likely to reflect fundamental anatomical features of cortical circuitry. One might therefore expect that even with training-related changes in cortical physiology the point image would be largely conserved, i.e., that changes in topography would have the opposite sign as changes in receptive field size. This
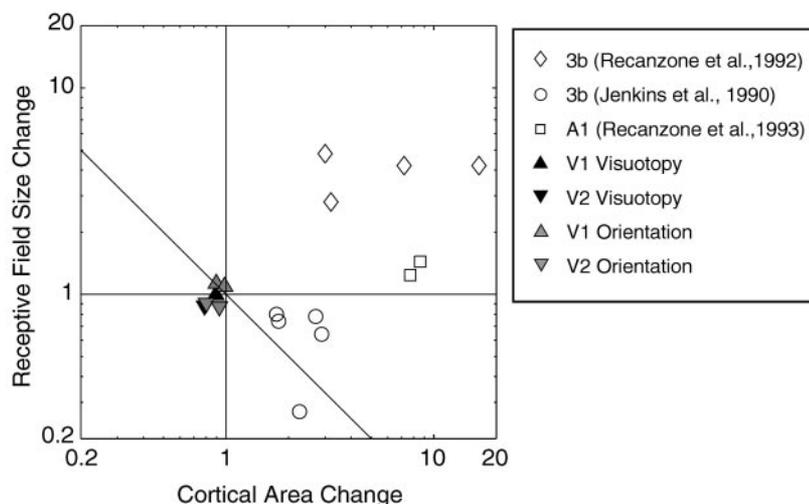

FIG. 15. Topographic and receptive field changes compared to previous perceptual learning studies in auditory and somatosensory cortex. Each point indicates the ratio of receptive field size and cortical area either before and after training and between trained and untrained representations. For the auditory training, receptive field size was characterized by the bandwidth Q10 (Recanzone et al. 1993). For orientation, receptive field size was characterized by the bandwidth b_θ of Table 2, and area was characterized by the preferred orientation distributions shown in Fig. 4. Animals are considered separately. The diagonal line indicates changes consistent with a conservation of point image size. Because our training was specific to both orientation and location, topography and receptive field extent were computed for both parameters (black triangles). Although there is some intersubject variability within studies, the largest changes are between different studies. Interestingly, two studies in the same cortical area indicate different effects on training: in one receptive field sizes increased with training (diamonds), while in the other they decreased (circles). In contrast, to the previous studies, our data (filled triangles) indicate minimal changes with respect to the 2 specificities of training, location (black) and orientation (gray).

expectation is marked by the diagonal line in Fig. 15. There is little quantitative consistency between the studies in this regard. While our data, by virtue of the lack of any significant training-related changes, and the data from Jenkins et al. (1990b) are roughly consistent with a conservation of point image, the two other studies are not. Tactual-motor training also increases cortical area while decreasing receptive field size in area 3b, consistent with the conservation of point image (Xerri et al. 1999).

Figure 15 shows similar results when orientation is considered (gray triangles). In this case, receptive field size was characterized by the average bandwidth, and cortical area was characterized by the proportion of cells with similar optimal orientations. To assess the effects of training with respect to orientation, data from both the trained and untrained representations were combined and separated according to optimal orientation. The "size" and "area" in orientation space of cells within 22.5° of the trained orientation was then compared to all other cells. Our data indicate no obvious change in either metric for V1 or V2. Although our estimate of orientation "area" is indirect, it is consistent with a deoxyglucose study that reported little change in the size of orientation columns with orientation discrimination training (Schoups et al. 1995a). It seems likely that the particular design and characteristics of the training are likely to be important in determining cortical changes, since the two previous studies that were conducted in the same cortical area (Jenkins et al. 1990b; Recanzone et al. 1992b) are inconsistent.

Although experiments done in different sensory modalities necessarily involve different methods, we do not believe that these considerations are sufficient to explain the difference in results. In both the somatosensory experiments, receptive field size was plotted by hand for each cell using just-visible skin indentation. Because both experiments were done in the same laboratory, the techniques used in the two studies are presumably similar. Yet in one of these studies receptive field size decreased (Jenkins et al. 1990b), while in the other it increased (Recanzone et al. 1992b). Moreover, the magnitude of the training effects in the study showing the most dramatic effects is very large (Recanzone et al. 1992b): area changes up to a factor of 16, and receptive field size changes up to a factor of 4.8.

Another difference is that owl monkeys were used in the auditory and somatosensory studies. We do not believe that species differences are likely to be the primary determinant of training-related plasticity effects. Adult cortical plasticity has been demonstrated in rhesus macaques in retinal scotoma studies. Moreover, the previous studies are quantitatively inconsistent despite the fact that they all used owl monkeys.

One possible difference between the somatosensory studies and the present study is the area of cortical area that represented the trained stimuli. It has been suggested that there is an anatomical-based limit of 600–700 μm in the cortical extent over which training-related changes can occur (Jenkins et al. 1990a). If this is true across all of cortex, then changes resulting from a task that involves a large amount of cortex would have a smaller relative influence on the representation than changes associated with a task involving a small region of cortex. If we assume that somatosensory stimulation was confined to ~5 by 5 mm region (a finger pad), then, given the linear magnification factor near the digit tip of 0.18, the linear

extent of area 3b activation should be around 0.9 mm (Sur et al. 1980). If we define the size of our stimulus according to the 2σ border of the Gabor, then an area within ~3 mm line was activated during training of our study. If a maximum of 600 μm for map relocation is assumed, then 1.5 mm could represent the stimulus after somatosensory training, while in V1 the trained representation could be expanded to 3.6 mm. Thus the somatotopy linear magnification factor would increase by 67%, while the visual magnification factor would increase by only 20%. As can be seen in Fig. 10, our methods are probably not sensitive enough to reveal such a change (log difference = 0.08) in visuotopy within only 1° of the training center. However, because of the fixed orientation of our stimuli and the organization over the cortical surface for orientation, a continuous 10 mm^2 patch of cortex was not well activated by our training stimuli. Instead the stimuli activated small regions of similar orientation (~0.03 mm^2). Thus, even with a 600-μm limit in functional reorganization, changes in the distribution of preferred orientation should be readily observable with our methods. However, as shown in Fig. 4, any changes in the distribution of preferred orientation were modest.

In addition to the physiological differences, there were also differences in the behavior that arose from training. Our training was selective for both orientation and location. Similarly, Recanzone et al. (1992a,b) trained monkeys on a tactile discrimination task that was selective for both frequency and skin location. The perceptual improvement that we observed was orientation, but not location specific. On the other hand, the perceptual improvement reported by Recanzone was location, but not frequency, specific. In both cases, the specificities of the training do not match those of the perceptual improvements. However, the learning selectivity of our study is the opposite of that reported by Recanzone: ours does not involve changes in the mapping of the receptor sheet (retinotopy), while the Recanzone study does report such changes.

Differences in either the spatial extent of attention or the amount of attention devoted during the training process might be responsible for these behavioral and physiological differences (Ahissar and Hochstein 2000). However, if we assume that task difficulty largely determines the amount of attention devoted to a task, then the amount of attention is unlikely to explain the differences between our study and previous studies. In the auditory training, performance was kept between 65 and 75% during training, which was similar to our target range of 75–80% correct. Moreover, both the auditory and somatosensory training showed roughly the same rate of behavioral improvements during training that we observed (Recanzone et al. 1992a, 1993). It is also unlikely that visual attentional mechanisms used in perceptual learning are fundamentally different from those of other sensory systems: human imaging studies have shown attentional modulation in both primary auditory cortex (Jancke et al. 1999; Lewis et al. 2000) and primary somatosensory cortex (Johansen-Berg et al. 2000; Noppeney et al. 1999; Steinmetz et al. 2000). Moreover, the spatial extent of attention does not seem to be a major factor in this case, since the introduction of distractors during training (*monkey 2*) produced little difference behaviorally or physiologically.

It is possible that the visual system may differ fundamentally from other sensory systems. Selective deafferentation experiments give some support to this argument. While local retinal

lesioning produces little visuotopic remapping in the lateral geniculate nucleus (Darian-Smith and Gilbert 1995; Gilbert and Wiesel 1992), peripheral deafferentation has large effects in the thalamic nuclei providing input to somatosensory cortex (Faggin et al. 1997; Garraghty and Kaas 1991; Jones 2000; Nicolelis et al. 1991; Pettit and Schwark 1993). This suggests that plasticity effects may occur at a higher level in the visual system than in other sensory systems. This possibility is also suggested by a recent study in which neither the retinotopy nor receptive field properties of primary visual cortex were changed by line bisection training (Crist et al. 2001), despite location- and orientation-specific behavioral improvement.

There is also the possibility, suggested by the two area 3b studies, that changing the specifics of visual training might alter the physiological correlates of perceptual improvements. For example, our training in multiple visual dimensions might have precluded tuning changes in early visual areas (Zhang and Sejnowski 1999). This could be tested by training monkeys in the same task across a wide range of orientations and looking for location specificities in behavioral performance and physiology. Alternatively, it might be that our training was not specific enough. The stimuli used in our training were slightly larger than V2 receptive fields and significantly larger than V1 receptive fields. Therefore, in order to see large changes in the early visual areas, it might be necessary to train over a more restricted portion of visual space that better matches the spatial receptive field size of V1 and V2. The reduction in the size of the representation of trained stimuli might also make reorganizations limited to 600 μm more detectable. It will require further study to determine whether the poor correlation between visual cortex physiology and behavioral improvement we have observed is fundamental to the visual system or merely specific to the particulars of our training paradigm.

Neuronal decision models

Although behavioral performance in our task ultimately depends on the activity of neurons in early visual areas, it is not known how such activity leads to decisions. Moreover the changes that occur during training introduce an additional level of complexity. Changes in performance as a consequence of practice can arise from greater familiarity with the task, a change in the sensitivity of neurons in these early areas, or a change in the pooling of signals from these early areas. We do not believe task familiarity is an issue since prior to orientation-specific training, the monkeys were familiar with the match-to-sample task.

Although previous studies have suggested that improvements in fine spatial discrimination would necessarily involve early areas of visual cortex (Ahissar and Hochstein 1997), it should be emphasized that in some cases changing low-level representations could severely impair normal vision. For example, if the behavioral pattern shown in Fig. 14 reflected a task-invariant change in representation, then the monkey would be unable to discriminate large differences in orientation. Given these problems, it would seem undesirable to change early representations so as to improve performance in a particular task unless there was no alternative. Our data suggest that a change in the early visual areas was not responsible for observed behavioral improvements for two reasons: *1*) although we observed some slight orientation and location-specific effects in V1, the behavioral improvement was orientation specific and only slightly location specific, *2*) pooling models indicate that any orientation biases in our neuronal populations were insufficient to explain the orientation specificity of performance. Thus, even in the demanding and specific orientation task used in our training, physiological changes in the earliest levels of visual processing were not required to improve performance.

To examine whether the improved behavioral performance is likely to result from physiological changes in V1 and V2 or from changes in higher visual areas, we needed to compare the physiology with our behavioral measurements across different orientations and locations. In this case physiology means the complete physiological state of the early visual areas when our stimuli were presented.

To explicitly test the performance of pooling models over a range of orientations, we used the optimized (i.e., orientation-biased) pools constructed from the trained V1 population. Because adding neurons or introducing noise will affect performance across the entire orientation space, these changes will not significantly alter the *pattern* of performance over stimulus space: for any given pool size performance is better at the trained orientation (Figs. 12 and 13*C*) than the untrained orientation (Figs. 12 and 13*D*). As expected given the orientation bandwidths of single cells (Fig. 5, *A* and *B*), these models predict excellent performance across all orientations for nonmatch differences larger than 20°, even with a pool of neurons specifically chosen for performance at the trained orientation (45°). Indeed, the only circumstances under which performance is poor in these models is for small changes in orientation around 135°. It is important to note that if the population is suboptimal, that is, not entirely composed of cells whose preferred orientation is around the trained orientation, the range of high performance will expand and performance around 135° will improve. This would make the pooled performance even more discrepant with the observed behavior (*A*). The only way a discrimination model would produce poor performance for a large range of orientations is if few neurons were pooled (Figs. 12 and 13*D*). However, such a small pool would be insufficient to produce the level of performance seen at the trained orientation (Figs. 12 and 13*C*). Thus discrimination based on early visual area responses cannot easily explain the animal's behavior.

One distinction between our study and others is that in our case the performance obtainable from individual neurons is far worse than the animals' performance. In previous models, the converse is true: the performance of some individual neurons exceeds that observed behaviorally (Britten et al. 1992; Prince et al. 2000). The challenge in these previous models is to explain how such neuronal signals can be degraded by the introduction of noise or neuronal correlation, while in our case the challenge is to explain how neuronal signals can be improved in an orientation-selective manner. It is possible that neuronal signals more appropriate for our observed behavioral patterns could be found at higher levels in the visual system that also contain orientation-selective neurons, such as V4 or inferotemporal cortex (IT) (Vogels and Orban 1994b). In this case our pooling models may be physiologically manifested in the form of single-unit selectivities in higher visual areas: neurons that can reliably and accurately discriminate orientations around 45°, but not other orientations. As mentioned

above, we would expect such selectivity to be task dependent in order to limit the negative consequences of such an algorithm. Task-dependent firing in an orientation discrimination task has been reported in IT neurons, but, in a study of the effects of orientation-specific training on such neurons, no strong orientation biases were observed (Vogels and Orban 1994a). We are currently investigating the possibility that stronger physiological correlates might be present in areas V4 and later stages. However, because V1 ultimately provides the predominant source of visual input to higher visual areas, any higher-order pools would depend on V1 activation and would therefore not alter the conclusions of our models.

Performance was poor for base orientations different from the trained orientation, even when the orientation change was large (>30°). These data do not necessarily suggest that training causes a worsening of inherent discriminative capabilities of the animal subjects (Mato and Sompolinsky 1996). If such a large decrement in discrimination performance was independent of task, it would likely adversely affect normal behavior. Instead we feel the behavioral pattern of Fig. 14A reflects task strategy, and would therefore not be visible outside probe trials. Poor performance after orientation transitions in humans has similarly been attributed to task strategy (Fahle and Edelman 1993). The only model that matched the pattern of behavioral performance observed over this range of orientations was an orientation-selective pooling model in which decisions were based on a orientation classification, rather than a discrimination per se. In both of these respects, our pooling model is distinct from previous attempts to relate single unit selectivities to visual behavior: prior models made use of unbiased pooling, in which neurons were included irrespective of their appropriateness for the perceptual task, and decisions were based on discriminating two pools of neuronal responses (Britten et al. 1992; Prince et al. 2000; Shadlen et al. 1996). Fundamentally these differences arise from the discrepancy between the orientation selectivity in our neuronal populations and the observed behavior. The lack of significant orientation bias in the neuronal populations mandates a selective pooling, while the poor performance of the animals at non-trained orientations dictates that decisions are based on classification rather than discrimination.

Because our study is the first to compare discrimination and classification pooling models using the same data set, it is unclear whether previous "discrimination" tasks might in fact be well described by classification-based models. For example, in the motion discrimination task of Britten et al. (1992), monkeys had to make an up-down decision regarding the direction of threshold strength motion. Although in their modeling this decision was arrived at by discriminating the activity produced by a "down" pool with that of an "up" pool, one might also imagine the monkeys used a neuronal pool to directly classify the stimulus as "up" or "down." It is also unclear whether classification-based decision making is more prevalent or natural than discrimination-based decisions for match-to-sample tasks. For example, our monkeys may be "classifiers" because in their initial orientation discrimination training they were presented with horizontal and vertical stimuli. This might have encouraged the establishment of two stimulus categories (above 45 and below 45°), which were then refined during the course of training. Alternatively, there might be some intrinsic advantage toward classification as opposed to

discrimination such that the behavioral pattern of Fig. 14A would emerge even if initial training was done in an unbiased manner. For example, orientation identification is more resistant to IT lesions than is orientation discrimination (Vogels et al. 1997) and involves the activation of a larger number of brain regions in humans (Orban et al. 1997). Training might also be of fundamental importance. Although short-term psychophysical improvements were seen in the motion discrimination tasks (Zohary et al. 1994), in these prior studies there was no long-term effort over many months to improve thresholds. Thus even if there is not a natural bias toward match-to-sample decisions being based on classification in normal circumstances, such a bias might exist for perceptual learning (Herzog and Fahle 1998) or when selective neuronal pooling is invoked.

The diversity of specificities found in different visual learning tasks has prompted the suggestion that the physiological locus of such learning is highly dependent on the nature of the task. Training for "higher-level" tasks tends to be faster and more generalized than training for "low-level" tasks (Ahissar and Hochstein 1997; Fine and Jacobs, personal communication). The definition of low-level is necessarily of critical importance to this conclusion: it is usually defined by training whose specificities correspond with the sensitivities of single neurons in early visual areas. Under this definition, our training, which involved orientation discrimination and was restricted in spatial location and orientation, would meet the definition of low-level. However, our data indicate that such a low-level task cannot be easily explained by changes in early visual areas, but can be by a selective higher-level pooling. There is also psychophysical evidence that suggests changes in the earliest visual areas cannot solely explain training-related improvements in visual perception, and that improvements in orientation discrimination in the presence of noise are likely to arise from changes in the pooling of low-level detectors rather than changes in the detectors themselves (Dosher and Lu 1998, 1999). Because activity in V1 is ultimately responsible for all visual-guided behaviors, changes at the earliest levels would imply considerable transfer between tasks. However, several perceptual learning experiments have reported poor transfer of perceptual improvements between different tasks at the same location (Ahissar et al. 1998; Crist et al. 1997; Fahle and Morgan 1996). Furthermore, changes at the earliest levels of visual processing, because of their necessary impact on all aspects of visual processing, might not be desirable. As mentioned previously, normal vision would be severely impaired if the specificity of orientation discrimination observed within in our task was always present as a result of changes at the earliest level of visual representations. Because the stimuli in our training were well-suited for the neuronal selectivities of these early visual areas, our data suggest that the physiological locus of perceptual learning is not strictly governed by a correlation between the selectivities seen in single neurons and the specificities of the training.

APPENDIX: NEURONAL POOLING MODELS

We constructed ideal detector models in which the signals from the neurons that we recorded from are combined in the absence of noise. We separately applied these models to each of our four neuronal populations (trained and untrained location in V1 and V2) for 6°

orientation discrimination tasks. We also applied these models to modified optimized populations in which the peak orientation for each cell was shifted to maximize discrimination and classification around 45°, but all other parameters (bandwidth, response rate, and spatial frequency tuning) were maintained. For both discrimination and classification, optimized pools were constructed by shifting one-half of the neurons so their peak orientations were aligned below 45° to be optimal for the 43° stimuli, and the remaining half were shifted above 45° to be optimal for the 48° stimuli (Fig. 11). Models were evaluated with pool sizes of 1, 5, 10, 20, 50, 100, 200, and 500 neurons. For each pool size, 40 random samplings of neurons were tested.

For each neuronal population, we evaluated the performance of an ideal observer of that population assuming that each neuron was an independent detector. Two types of pooling were tested. In the first, we assumed that the ideal observer simultaneously observed all of the neurons to arrive at a decision. We term this detector pooling. If we assume that each neuron i is independent, then the discriminability is (Green and Swets 1988)

$$d = \sqrt{\sum_i d_i^2}$$

For the probability model, the ideal observer makes a match decision if the distribution of decisions among all the detectors is more likely to be associated with a match. For the case of probability pooling, there are two alternatives: *1*) the task probabilities are pooled or *2*) the probabilities for each stimulus classification are pooled, and then a match/nonmatch decision is made on the basis of these stimulus classifications. In all of the decision pooling models, the best detectors contribute disproportionately to the decision.

An alternative is to pool stimulus responses before a decision by the ideal observer, which we term response pooling. It is this model that has been most often applied to neurophysiological data. The exact same formulas as above can be used, substituting a pooled population response for the individual neuronal responses

$$r(\theta, f) = \sum_i r_i(\theta, f) \quad \text{and} \quad V(\theta, f) = \sum_i K_i r_i(\theta, f)$$

We tested five decision pooling models: two discrimination models in which neuronal responses are compared to a single threshold to arrive at high/low orientation decisions (Fig. 11, *A* and *C*), and three classification models in which stimulus evoked signals are compared against all possible signals to determine whether a high or low orientation was presented (Fig. 11, *B* and *D*).

For discrimination-based decisions, two pooling models were considered: one in which a decision was based on a pooled response (Fig. 12), and one in which a decision was based on decision pooling among the individual neurons (not shown). Figure 12 shows the performance of individual neurons and pools of those neurons for a orientation discrimination task in which the two orientations differ by 6°. In all observed and optimized populations, response pooling provided better performance (higher *d′*) capability than detector pooling. Both pooling models were able to provide performance comparable to trained performance with a sufficient number of neurons. However, the number of neurons necessary to reproduce the behavior at the trained orientation produces performance that far exceeds behavioral observations at the untrained orientation. Only by introducing an orientation bias, such that only cells with optimal preferred orientations are considered, can the performances from neuronal pooling exhibit a substantial orientation bias.

For classification, three pooling models were considered: *1*) individual neurons are considered as match/nonmatch classifiers, and their performance is pooled (not shown); *2*) individual neurons are considered as high/low orientation classifiers, and their performance is pooled to arrive at a match/nonmatch decision (Fig. 13); and *3*) neuronal responses are pooled to arrive a orientation classification that is then used for the match/nonmatch decision (not shown). Any one of these models, with sufficient cell numbers, is capable of producing a single behavioral performance level. For our purposes, it is the comparison of pool performances between different neuronal populations that is relevant. A selective pooling of cells with optimal orientations must be invoked, irrespective of any particular pooling model, to replicate the behavioral orientation bias. Even after the implementation of such an orientation-selective pool, only one decision/pooling model (Fig. 14*D*) was able to replicate behavioral observations (Fig. 14*A*). For this model, decisions were arrived at by classification, and response pooling was used prior to classification. Because this latter model essentially reduces the pool size over which decisions are made, it has the greatest dependence on orientation with relatively poor performance outside the range of orientation that was trained, even when the orientation difference was large. Other classification models exhibited superior performance (and therefore a poorer fit to the behavioral data) because they allowed the signals from each neuron to be fed into a decision maker before pooling (detector pooling).

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