



# Learning to see: experience and attention in primary visual cortex

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The response properties of neurons in primary sensory cortices remain malleable throughout life. The existence of such plasticity, and the characteristics of a form of implicit learning known as perceptual learning, suggest that changes in primary sensory cortex may mediate learning. We explored whether modification of the functional properties of primary visual cortex (V1) accompanies perceptual learning. Basic receptive field properties, such as location, size and orientation selectivity, were unaffected by perceptual training, and visual topography (as measured by magnification factor) was indistinguishable between trained and untrained animals. On the other hand, the influence of contextual stimuli placed outside the receptive field showed a change consistent with the trained discrimination. Furthermore, this property showed task dependence, only being manifest when the animal was performing the trained discrimination.

Cortical plasticity is likely involved in the normal cognitive processing of adult animals, and is important even in the functioning of primary sensory areas<sup>1</sup>. Whereas plasticity may underlie functional recovery following CNS lesions, it may also mediate functional changes accompanying experience and learning. Several characteristics of perceptual learning suggest the involvement of early stages in sensory processing, perhaps even as early a stage as primary sensory cortex. Evidence in support of this idea has been found in the somatosensory and auditory systems<sup>2–4</sup>. Primary sensory cortex is a useful model for learning because its underlying mechanisms—its circuitry, functional architecture and receptive field (RF) structure—can be accessibly studied.

Various cortical changes both are associated with improvement in perceptual performance and occur in primary sensory cortices<sup>2–4</sup>, which suggests that the mechanisms of learning may be general to the neocortex as a whole. Independent studies of plasticity of RF properties and functional architecture of primary visual cortex (V1) heighten the possibility that plasticity associated with perceptual learning might occur there. Whereas certain RF properties such as ocular dominance are mutable only during a limited critical period early in postnatal development<sup>5</sup>, a number of other properties, most notably, visual topography and RF size, can be influenced by visual experience throughout life<sup>1</sup>.

In the visual system, psychophysical evidence shows that training can improve discrimination stimulus attributes, including position, depth, orientation, motion, texture, spatial phase and hyperacuity<sup>6–11</sup>. In a previous study, we showed that practice with a particular visual discrimination task, three-line bisection, produces a substantial improvement that is specific to the trained stimulus<sup>12</sup>. The specificity for position and orientation suggests that the early stages of visual processing are involved in the learning of this task. To determine whether V1 is involved in the learning of such visual discriminations, we trained two macaque monkeys to perform the same bisection task used with human subjects, and we recorded from cells in area V1. We examined the RF properties and the map of visual space in trained animals for changes that might relate to perceptual training. In addition

to its classical response properties, a cell's response to a stimulus within the RF is modulated by the presence of additional stimuli around the RF, and this modulation depends strongly on the geometric relationship of the stimulus elements. We explored the tuning of cells to shifts in the lateral placement of two parallel lines with positions analogous to those of lines in the bisection task. Furthermore, we examined the influence of the behavioral state of the animal on these interactions.

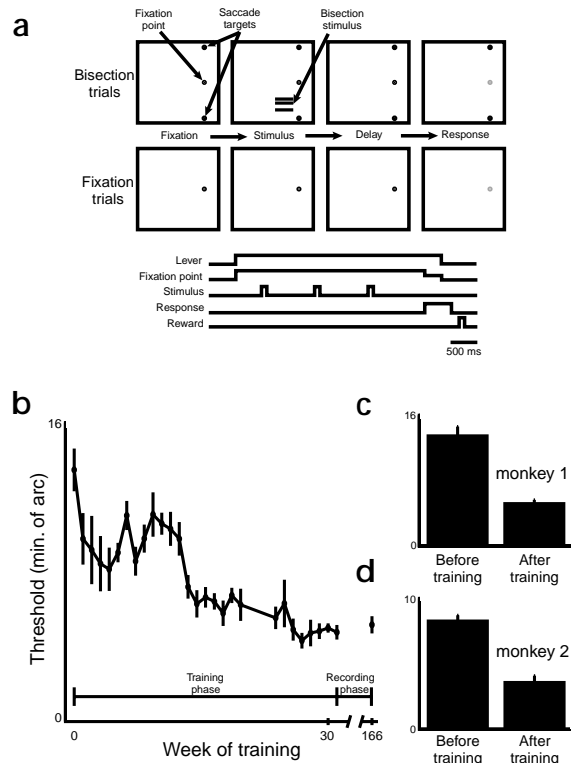
## RESULTS

**Monkeys improve bisection discrimination with training**  
Both monkeys showed substantial improvement in bisection performance with training. Over the course of 30 weeks of training, monkey 1 showed a threshold reduction greater than a factor of three (Fig. 1c), and monkey 2 showed a 57% threshold reduction (Fig. 1d).

Monkeys were trained with a series of tasks that approximated the final bisection task. The initial threshold (Fig. 1b) was measured during the first week of training on the bisection task itself, and some learning may have occurred before this time. During the recording phase, the monkey had fewer opportunities to practice the bisection discrimination, but the threshold measured several months after electrophysiological recordings began shows that the improved performance was maintained over this period (Fig. 1b).

## Cortical magnification does not change with training

One of the most striking effects of perceptual training in the somatosensory and auditory modalities<sup>3,4</sup> is the remapping of the cortical representation of the sensory surface such that a much larger region of cortex is responsive to stimulation of the trained region. To examine whether a remapping of visual space accompanied the learning of the bisection discrimination task described above, we constructed a topographic map of the cortex of the trained monkeys from recordings of superficial layer cortical cells. The location of the RF center of an isolated unit was determined by recording the response to the flashing of a small bar in a pattern



**Fig. 1.** Monkeys improved with training on bisection task. **(a)** The tasks that monkeys were trained to perform. Top, a single bisection stimulus presentation as it was shown to a monkey. Bottom, fixation task in which the monkey was merely required to maintain fixation until the fixation point was dimmed. Beneath the images of the stimuli are traces indicating the time course of stimulus presentation. **(b)** Thresholds measured for monkey 1 for each week of training. During the recording phase, the monkey received less bisection training, but improvement was retained. **(c)** Before and after training thresholds measured for monkey 1. **(d)** Before and after training thresholds measured for monkey 2.

in the cortex of naive monkeys<sup>18</sup>, indicating that no substantial increase occurred as a result of perceptual training.

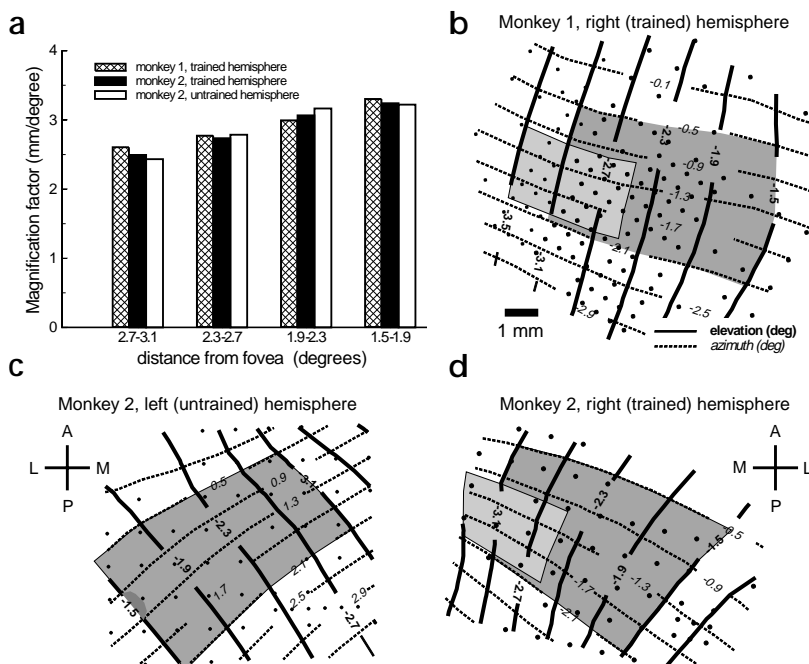
A similar map was made from the trained hemisphere of monkey 2 (**Fig. 2d**). The magnification factor at the cortical locus of the bisection stimulus was 19 min/mm, closely matching the value obtained in monkey 1. Though the values for the two monkeys used in our study match those reported for naive monkeys, the individual variation found in the cortical representation of space might permit more subtle changes to be missed in these comparisons. Therefore, we mapped the untrained hemisphere of monkey 2 (**Fig. 2c**). The magnification factors for various eccentricities in both trained hemispheres and the untrained hemisphere of monkey 2 were compared across the cortical region surrounding the bisection task; the values in all three hemispheres were almost identical (**Fig. 2a**).

of equally spaced locations both along and orthogonal to an axis defined by the orientation preference of the neuron. Recordings were made in a grid-like pattern in steps of 0.5 to 1 mm. The RF locations determined for 144 separate penetration sites in monkey 1 were used to estimate the appropriate position of isoazimuth and isoelevation lines surrounding the representation of the visual location where the bisection stimulus was presented (**Fig. 2b**). An estimate of cortical magnification of the area surrounding the trained location was obtained by calculating the square root of the number of square millimeters representing a  $1^\circ \times 1^\circ$  area of visual space<sup>17</sup>; the magnification factor was 20 min/mm for the cortical region representing the visual position of the bisection stimulus. This figure matches reported values for magnification at this cortical location

#### No change in receptive field size or orientation tuning

Along with substantial changes in the size of the cortical representation of the trained skin surface, changes in RF size have been reported to accompany the learning of a somatosensory discrimination task<sup>3</sup>. Thus, we asked whether changes in RF size in V1 accompanied learning of the bisection discrimination. We flashed a small bright bar in locations spanning the area of the RF along the orientation axis, and calculated RF size as the center-to-center distance between the outermost stimulus bar locations showing response above spontaneous levels. The mean RF

**Fig. 2.** Representation of visual space did not change as a result of bisection training. **(a)** Comparison of cortical magnification factor measured at several locations surrounding the representation of the trained visual location. **(b)** Map of cortical area representing the region of space where the bisection stimulus was presented during training ( $3.25^\circ$  parafoveal). Isoazimuth and isoelevation lines are drawn based on the RF positions measured for each penetration site (black dots). **(c)** Cortical map of untrained hemisphere of monkey 2. **(d)** Cortical map of trained hemisphere of monkey 2. Light gray areas in **(b)** and **(d)** indicate region where bisection task was represented. Dark gray areas in **(b-d)** show area over which magnification factor was calculated for panel **(a)**.





**Fig. 3.** RF size and orientation tuning bandwidth did not change following bisection training. RF size was determined using the minimum response field technique (see Methods). **(a)** Comparison of RF size in trained and untrained monkeys. Left bar indicates mean RF size in monkey trained on bisection discrimination ( $n = 139$ ; monkey 1, 119 units; monkey 2, 20 units). Right bar indicates mean RF size in untrained animals ( $n = 51$ ). **(b)** Orientation tuning in trained and untrained monkeys. Left bar shows mean width of orientation tuning curves in two trained monkeys ( $n = 108$ ; monkey 1, 87 units; monkey 2, 21 units). Right bar indicates the mean value of tuning width in untrained animals ( $n = 63$ ).

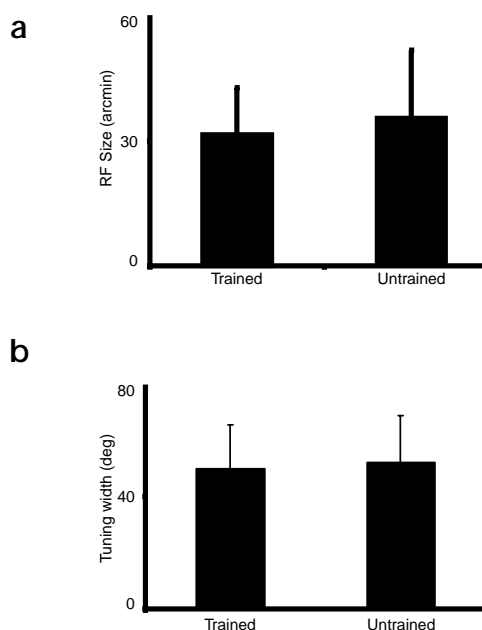
size was calculated for two trained and two untrained monkeys for neurons at eccentricities near that of the bisection stimulus used with the trained animals (between  $2^\circ$  and  $4^\circ$ ); RF size in trained and untrained animals did not differ (Fig. 3a).

Cells in V1 are also particularly sensitive to the orientation of edges and line stimuli. Selectivity for orientation has been proposed to be involved in hyperacuity discriminations. However, we found similar orientation tuning bandwidth of cells in cortex of trained versus untrained animals (Fig. 3b).

#### Task dependence of contextual interactions

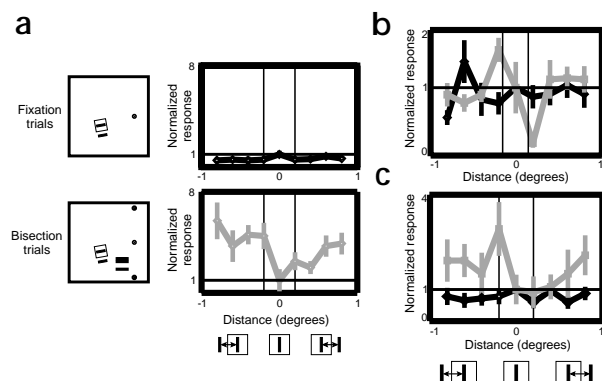
Because standard properties such as magnification factor, RF size and orientation selectivity were unaffected by training, we explored possible changes in higher-order properties such as contextual tuning. Cells in V1 are sensitive to patterns more complex than oriented line segments<sup>19</sup>. The effect of placing additional lines outside the classical RF of a cell depends on the precise geometric relationships between the elements of the stimulus pattern. For example, a single collinear line presented outside the classical RF along the orientation axis often provides facilitatory input to a unit responding to an optimally oriented line within its RF<sup>20</sup>; when placed in a side-by-side configuration, the line outside the RF has an inhibitory influence<sup>21,22</sup>. We therefore examined whether contextual patterns in the three-line bisection stimulus uniquely affected the responses of visual cortical neurons in trained animals.

We centered an optimally oriented bar in the RF, and measured the response to a second, parallel bar presented in a flanking position, similar to the side-by-side arrangement of lines in the bisection stimulus. Because the monkeys were trained to perform both a fixation task and a bisection task, we could examine the responses of our units while an animal was performing different visual discriminations. We measured changes in the responses of neurons with RFs near the trained location of the visual field, and compared the changes based on the task the

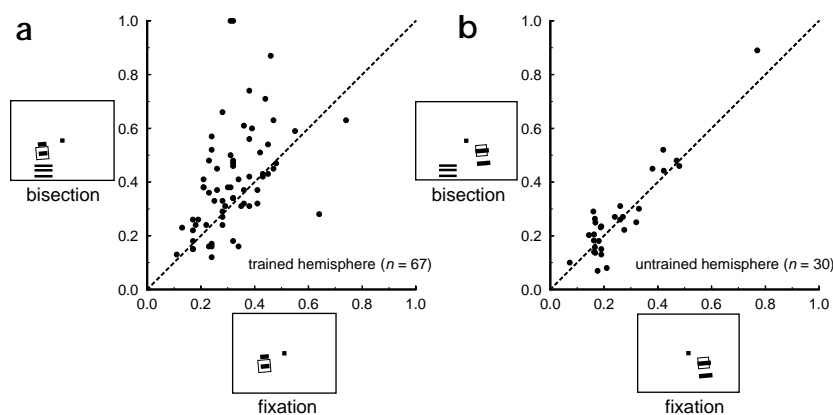


monkey was performing. Two effects could be distinguished. First, the response rate of a neuron was slightly reduced when the monkey was instructed to perform bisection trials. This finding was not unexpected, as we have observed previously that when additional stimuli (in this case, the bisection stimulus) are placed in the neighborhood of the RF, the response of the cell is inhibited. The most striking effect, however, was that the shape of the tuning curve for the modulation produced by a flanking bar was very different when the monkey was performing the bisection task than when it was performing the fixation task. In fixation trials, the response of a typical neuron was reduced by the presence of a flanking bar on either side of the RF (Fig. 4a, top right). When the monkey was performing the bisection discrimination, the effect of the flanking bar changed dramatically from inhibition to facilitation, and the facilitatory effect depended on the distance between the two bars (Fig. 4a, bottom). Furthermore, the extent of facilitation was asymmetric; the facilitatory effect of a flanking bar was stronger on one side of the RF.

This effect was even more dramatic for a second cell (Fig. 4b), in which presenting a flanking bar on one side of the RF during bisection trials produced a substantial facilitation, whereas pre-



**Fig. 4.** Contextual interactions changed when the monkey performed the bisection task. **(a)** Left, stimulus arrangement used to examine contextual interactions during the performance of fixation and bisection trials. Dotted line indicates borders of RF. Upper right, tuning curve of one cell to the placement of parallel bars while the monkey was performing a fixation task. Response rate of cell to all stimuli has been normalized by the response rate obtained by placing a single optimally oriented bar inside the RF. Lower right, tuning curve of the same cell for the same set of parallel bar stimuli while the monkey performed bisection trials. **(b)** Example of the tuning of another cell for parallel bar stimulus. **(c)** Example of the tuning from a third cell for parallel bar stimulus. Black lines indicate responses obtained when the animal was performing the fixation task. Gray lines indicate tuning during bisection trials. In the tuning curves, the vertical lines represent the boundaries of the receptive fields determined by the minimum response field technique (see Methods). These boundaries did not change with bisection versus fixation trials. Error bars, s.e.m.



**Fig. 5.** Modulation depended on the task that the monkey performed in trained but not untrained hemisphere. **(a)** Modulation during bisection and fixation trials. Amount of modulation observed for different units when the monkeys were performing the bisection task in comparison to the amount of modulation when the animals were performing fixation trials ( $n = 67$ ). **(b)** Monkey performed bisection task on trained hemisphere, and test stimuli were presented to cells in untrained hemisphere. Modulation did not depend on the behavioral condition for cells in the untrained hemisphere.

presenting the bar on the opposite side caused a profound inhibition of the unit's response. The shape of the tuning curve for flanking interactions during bisection trials varied considerably from cell to cell (Fig. 4a–c).

The wide variety of tuning shown by different cells for flanking interactions during bisection performance challenged us to develop a method of comparing the responses over the recorded population. The amount of facilitation or inhibition produced by the flanking bar was greater when the animal was performing bisection trials than when it was performing fixation trials. To describe this effect for the population of neurons, we defined a measure of the strength of these modulatory interactions.

$$\text{modulation} = \frac{\text{maximum normalized response} - \text{minimum normalized response}}{\text{maximum normalized response} + \text{minimum normalized response}}$$

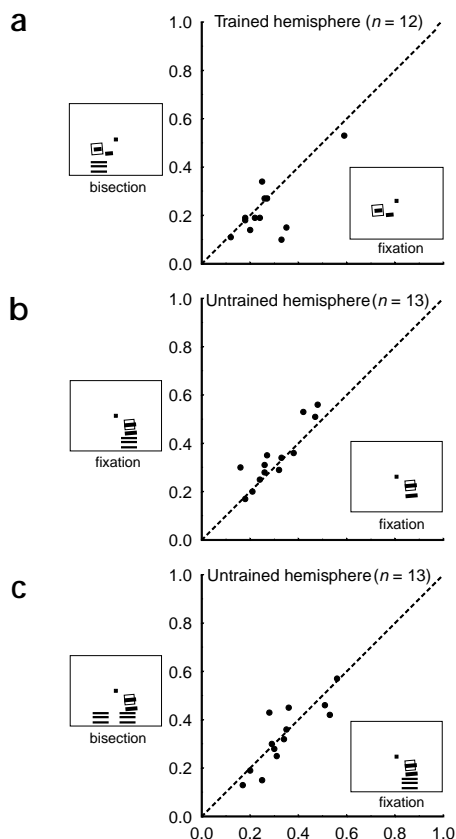
Modulation is a measure of the influence of the parallel bar on the cell's response to a bar centered in its RF. By definition, modulation ranges from zero (the response to single bar was not influenced by the presence of the additional bar) to one (the response was facilitated by an additional bar in one position and inhibited by the additional bar in another position). The amount of modulation observed for 67 cells while the monkey performed bisection trials was plotted against the modulation observed under fixation trials (Fig. 5a). The difference in the distribution in modulation in the trained hemisphere between fixation and bisection trials was highly significant ( $p < 0.0002$ ,  $t = 3.95$ , paired  $t$ -test).

Most cells examined in the experiment described above had RFs near but not overlapping the visual location where the bisection stimulus was presented during training. The appearance of training effects in the region surrounding the trained location is in agreement with psychophysical evidence from human observers demonstrating that bisection discrimination training improves performance within a couple of degrees of the trained location<sup>12</sup>.

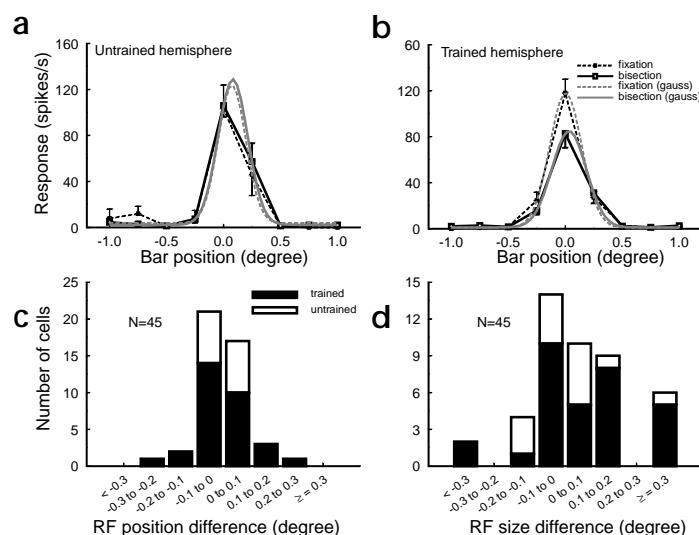
**Fig. 6.** Changes in contextual interactions are not observed for untrained stimulus patterns or in the untrained hemisphere. **(a)** Task dependence of contextual interactions was only seen for patterns present in the trained stimuli. Modulation by a collinear line showed no effect of behavioral condition. **(b)** Monkey performed a fixation task while test stimuli were presented in untrained hemisphere in the presence of bisection-like stimulus. The presence of a bisection-like stimulus did not lead to changes in modulation. **(c)** Monkey performed bisection task in trained location while test stimuli and bisection-like pattern were presented to cells in untrained hemisphere. Modulation of cellular responses in the untrained hemisphere did not depend on behavioral condition.

Bisection performance diminishes with distance from the trained location, suggesting that cells in cortical areas remote from the trained location should not show the task-dependent changes in modulation. Contrary to what we observed in the trained hemisphere, in the untrained hemisphere, the modulation of cellular responses by a parallel line was similar during the bisection and fixation tasks (Fig. 5b). The difference in modulation under bisection between the trained and untrained hemispheres was significant ( $p < 0.05$ ,  $t = 2.22$ , two-sided  $t$ -test), and the difference in modulation in the untrained hemisphere between fixation and bisection was not significant ( $t = 1.07$ ,  $p = 0.29$ , paired  $t$ -test).

Contextual interactions have been shown to be influenced by spatial attention<sup>23</sup>. Clearly, the focus of attention changed from the center of vision to the peripheral location of the bisection







**Fig. 7.** Measurement of receptive field profiles during fixation and bisection trials in trained and untrained hemisphere. **(a)** Example of a cell from untrained hemisphere. Responses were measured for a single bar stimulus placed in various positions along an axis orthogonal to the RF orientation. Dark lines are fitted to the mean responses, gray lines are the Gaussian fits. Solid lines are measurements taken during bisection, and dashed lines are measurements taken during fixation. **(b)** Example of a cell from trained hemisphere, same conventions as in **(a)**. **(c, d)** Population analysis of cells from trained and untrained hemispheres, showing mean difference in RF position **(c)** and size **(d)** under bisection versus fixation. For this analysis, the RF position and width were obtained from the peak position and one standard deviation, respectively, of the Gaussian fits. Solid bars, trained hemisphere; open bars, untrained hemisphere. No significant difference was observed in either trained or untrained hemispheres.

task when our monkeys performed the bisection discrimination. If the change in contextual interaction were solely due to changes in the focus of attention, we would expect the modulation of cellular responses to other contextual patterns. Therefore, we examined the effect of performing the bisection task on the modulation produced by a collinear line presented in the RF surround, but little change in the modulation index was observed (Fig. 6a).

The finding that task-dependent changes were only seen for contextual patterns present in the trained stimulus suggests that the difference observed in contextual interactions described here was the result of the training the monkeys received. In our experiments, however, when a monkey was performing the bisection task, the test pattern was presented in the RF of the cell simultaneously with the bisection stimulus itself. This raises the possibility that the changes in cortical interactions we have described might be due to the difference in the stimulus pattern. If this were the case, however, the response of a cell to other local contextual patterns, such as the collinear line used in the experiment described above, would also change when the bisection pattern was present. This was clearly not the case (Fig. 6a). Further evidence of this fact comes from recordings in the untrained hemisphere, where the modulation of cellular responses was unaffected by the simple presence of the bisection stimulus (Fig. 6b). Finally, to further demonstrate that cells in untrained cortex did not show task-dependent changes in modulation, we determined whether the presence of a bisection-like stimulus in the untrained hemifield during bisection discrimination in the trained location would induce changes in the modulation of cells in untrained cortex. No such change was observed (Fig. 6c).

The above findings indicate that contextual interactions, and not the responses of cells to simple stimuli, were affected by training. However, given that the contextual interactions show task dependence, one might ask whether the standard RF properties of size, position and orientation might be similarly affected. We measured the RF profiles of cells under both fixation and bisection trials, and fitted these profiles with a Gaussian. The RF profiles were nearly identical under both behavioral conditions and in both the trained and untrained hemispheres (Fig. 7). Between fixation and bisection trials, no significant difference was found for RF position ( $n = 45$ ,  $t = 0.27$ ,  $p \approx 0.79$ ), RF size ( $n = 45$ ,  $t = -1.52$ ,  $p \approx 0.13$ ) or orientation preference ( $n = 20$ ,  $t = -1.67$ ,  $p > 0.1$ ).

## DISCUSSION

The suggestion that perceptual learning might rely on primary sensory cortex comes from the great specificity in the learning for position and orientation, attributes to which early stages in sensory processing are selective. The specificity of visual perceptual learning in itself is not sufficient to indicate the involvement of the early stages of visual cortical processing, because even cells in inferotemporal cortex can be induced to show selectivity for such properties<sup>24</sup>. Moreover, attention can reduce the size of a cell's RF in certain cortical areas<sup>25</sup> and therefore heighten the spatial resolution of tasks involving these areas. One also has to account for the specificity of perceptual learning to the context within which a discrimination is made. Because cells in V1 show selectivity for complex stimulus configurations, it becomes difficult to use complexity as a clue to determine the site of learning within the cortical hierarchy. In this vein, we note that learning to discriminate even very complex stimulus patterns can show some specificity for the location in which the stimulus was presented during training<sup>26</sup>.

Nevertheless, the suggestion that V1 might be involved in perceptual learning is reinforced by the demonstration of learning effects in other primary sensory areas, and one might expect common mechanisms to apply in cortical areas serving all sensory modalities. V1 is capable of remapping space under certain conditions—in particular, after retinal lesions<sup>27–29</sup>. No changes in cortical magnification, or cortical recruitment, were found in the current study to accompany training on the bisection discrimination, despite large gains in perceptual ability. Furthermore, we found the basic RF properties of size and orientation tuning to be unaffected by bisection training, even though analogous properties were modified in somatosensory and auditory cortex following training on vibration or pitch discrimination. The apparent difference in the mechanisms operating in different cortical areas may reflect the fact that our training involved emergent properties of cortical neurons, and showed specificity for context. In contrast, the changes in the somatosensory and auditory systems resulted from discrimination training on the input properties to the cortex, and therefore might not depend on intrinsic cortical circuits.

Increasing the amount of modulation invoked by visual patterns in the trained stimulus can easily be imagined to facilitate perceptual performance. It is noteworthy in this context that dur-



ing bisection trials, many cells were strongly facilitated by a parallel bar. In a study of contextual interactions in monkeys viewing passively, cells in untrained animals did not show facilitation for this pattern<sup>21</sup>. The absence of such facilitation in untrained animals strengthens the conclusion that these interactions were the result of bisection training. A substrate for these interactions exists in V1 in the axon collaterals of superficial layer pyramidal cells, which extend over several millimeters. These cells connect units of similar orientation preference<sup>30–33</sup> and are therefore well positioned to mediate interactions between the elements of the bisection stimulus used in our study. The ability of long-range horizontal connections to provide both excitatory and inhibitory input to their targets<sup>34–36</sup> is also suggestive of a role in the interactions described above. The implementation of perceptual learning by a selective modulation of subsets of horizontal connections allows for the specificity of the learning for the details of stimulus configuration. A mechanism of cortical recruitment would not have this property, and further, might be expected to lead to a decline in performance in the untrained portions of visual space represented by the adjacent cortical regions. This 'robbing' is not seen in the perceptual learning experiments.

The contextual influence that best represents the attribute involved in the bisection task is the modulation in the cells' responses to a second, parallel line placed at varying separation from a line placed centrally within the RF. The observed effects were specific for this property, because they were not seen for a different contextual influence, that of a colinear line at varying offsets. To make a stronger connection between the modulation index and the trained task, one can ask how the scale of the sensitivity to line separation measured for an individual neuron compares to the threshold in the bisection task. At the point at which neurons show their greatest sensitivity (the steepest part of the slope of the contextual tuning curves), the amount of change in the distance between the parallel lines that gives one standard deviation change in the firing rate is 9.75 minutes of arc, on average. The threshold in the task, after training, was four minutes of arc. The sensitivities are therefore roughly of the same scale, but the differences argue that some amount of pooling in the activity of the neurons is required to achieve the level of behavioral performance.

Perhaps the most striking aspect of the findings reported here is the apparent ability of the cortex to dynamically modify the processing of visual information according to immediate behavioral requirements. The monkeys in this study were trained to perform two different tasks: a simple dimming task and the three-line bisection discrimination. Lateral interactions in trained monkeys depended on the task the monkey was performing at the time. The task dependence of the contextual interaction permits the same neurons to mediate entirely different perceptual functions that may require opposing neuronal mechanisms. The inhibition of responses by parallel lines under the fixation task has been suggested to be involved in surface segmentation<sup>21</sup>. As shown here, this inhibition can switch to facilitation during the performance of the three-line bisection task. One would not want to design a system in which three-line bisection training would disrupt the subject's ability to segment the visual scene. To allow the performance of both tasks, one would either have to segregate the neurons mediating the task into separate functional compartments, or allow the same neurons to multiplex their function in a task-dependent fashion. The results of the current study suggest the latter solution. The further implication of this idea is that at the same time the cells change their RF structure, they change their line label, such that modulation in their firing is interpreted differently by the rest of the nervous system.

As a mechanism underlying the improvement in the bisection task, we propose a change in the strength and excitatory/inhibitory balance of a subset of horizontal inputs to V1 neurons. This modulation of the horizontal input would then vary according to the separation between the source and target neurons, therefore providing a greater modulation of the tuning to the separation of parallel lines. The contextual modulation would in turn be modulated by top-down influences, presumably mediated by feedback connections from higher-order cortical areas, to generate its task dependence. Thus, contextual influences within a particular cortical area may come not just from lateral connections within that area, but as an interaction between local circuits and feedback connections from higher-order cortical areas, thus providing a mechanism for both the stimulus selectivity and task dependence of the cortical responses to trained stimulus patterns.

## METHODS

Two macaque monkeys (*Macaca mulatta*) were trained and used to collect the physiological data reported here. During recording and training, monkeys were seated in a primate chair facing a computer monitor. The monkey's head was restrained using a surgically implanted stainless steel post. Eye movements were monitored using a scleral search coil system<sup>13</sup> (CNC Engineering, Seattle, Washington). During stimulus presentation, monkeys were required to maintain fixation within a 0.75–1.0° rectangular window; trials were aborted and reward was withheld if an eye movement greater than 0.5° was made. The actual variability in eye position from trial to trial was much less than that allowed by the fixation window. The mean position and standard deviation for typical experiments (based on a sample of data obtained during the recording of 21 units), relative to the fixation point, was  $0.07 \pm 0.03^\circ$  in azimuth and  $-0.02 \pm 0.05^\circ$  in elevation. Quality of fixation was the same during both fixation and bisection trials; the mean difference in eye position between fixation and bisection trials for typical sessions was  $0.03 \pm 0.04^\circ$  in azimuth and  $0.01 \pm 0.02^\circ$  in elevation. All procedures were conducted in compliance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals, and under approval of institutional review boards.

**Training.** Monkeys were initially trained to perform a simple fixation task (Fig. 1a). The animal was taught to initiate trials by pulling a lever attached to the primate chair. When the lever was pulled, a small bright spot was displayed on the screen, and the animal was required to maintain fixation on the spot until it was dimmed. If the monkey released the lever within a brief period of time following the dimming of the fixation spot, a small drop of juice was given as a reward.

To teach the monkeys to perform the bisection discrimination, we first trained them to perform a series of tasks designed to lead to bisection performance. The initial thresholds for bisection performance reflected the first thresholds measured for the final bisection task. In the bisection task, the monkey was presented with a set of three parallel horizontal lines (Fig. 1a). The monkey's task was to determine whether the central line was nearer to one or the other flank. During the presentation of the stimulus, the monkey was required to maintain fixation on a small spot. Following the presentation of the bisection stimulus, the fixation spot was extinguished and the monkey indicated its response by making an eye movement to one of two small spots presented at the top and bottom of the screen. Correct responses were rewarded with a drop of juice. The responses of the monkey to the bisection task were recorded and used to calculate the threshold of performance using the method of probits.

**Electrophysiological recording.** After training was complete, monkeys were surgically implanted with a steel chamber (inner diameter, 22 mm) enclosing a craniotomy over a portion of V1. Surgical procedures were done under aseptic conditions with pentobarbital sodium anesthesia. Recordings were made with glass-coated platinum iridium microelectrodes<sup>14</sup> with impedances between 1.0 M $\Omega$  and 3.0 M $\Omega$ . Using a stepping motor microdrive (Narishige, Tokyo, Japan), penetrations were made at typical intervals of 0.5 mm through the dura.



Recordings from single units were conducted daily in 2 to 4 hour sessions. After penetrating the dura, a rough RF map was obtained while the animal performed a fixation task. All recordings were made from the opercular surface of V1 at RF eccentricities ranging from 1.5° to 5.0°. Granule layers were identified by the characteristics such as high levels of spontaneous activity and brisk on/off response<sup>15,16</sup>. When such activity was encountered, the electrode was retracted to restrict recording to the superficial 600 µm of the cortex.

Neuronal activity was recorded over 600-ms epochs spanning the presentation of the stimulus. The level of background activity was measured for 200 ms, and a stimulus was then presented for 100 ms. During each trial, three to five 600-ms recording periods were conducted. For each cell, a time window was set within a range of 50–250 ms after stimulus onset depending on the latency and length of the response. The mean firing rate within this response window minus the spontaneous firing rate, calculated from the number of spikes obtained in the first 200 ms of the recording epoch, was used to determine the magnitude of the evoked response. The *t*-test was used to evaluate the significance of the evoked response.

Each recording session began by characterizing the RF extent and orientation preference while the monkey performed fixation trials. RF extent was determined by the minimum response field technique in which a small bar (typically 0.2–0.25° in length and 3 inches in width) was presented in steps (0.1–0.25° apart) either along the principal orientation axis of the cell to determine its length, or orthogonal to the orientation axis to determine its width. The distance between the outermost points that elicited a significant response was defined to be the size of the RF. For the comparison between RF profiles during fixation and bisection trials in trained and untrained hemisphere (Fig. 7), RF extent was determined by fitting the responses obtained at each position with a Gaussian and taking the standard deviation to be the size of the RF. Subsequently, contextual interactions were examined while the animal performed either fixation or bisection trials. During bisection trials, experimental stimuli were presented simultaneously with the bisection stimulus. The fixation and bisection trials were collected in separate blocks, and we collected 10 trials per stimulus condition. The tuning curves were calculated, and are shown along with standard error bars.

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