

Learning Strengthens the Response of Primary Visual Cortex to Simple Patterns

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Summary

Training can significantly improve performance on even the most basic visual tasks, such as detecting a faint patch of light or determining the orientation of a bar (for reviews, see [1, 2]). The neural mechanisms of visual learning, however, remain controversial. One simple way to improve behavior is to increase the overall neural response to the trained stimulus by increasing the number or gain of responsive neurons. Learning of this type has been observed in other sensory modalities, where training increases the number of receptive fields that cover the trained stimulus [3, 4]. Here, we show that visual learning can selectively increase the overall response to trained stimuli in primary visual cortex (V1). We used functional magnetic resonance imaging (fMRI) to measure neural signals before and after one month of practice at detecting very low-contrast oriented patterns. Training increased V1 response for practiced orientations relative to control orientations by an average of 39%, and the magnitude of the change in V1 correlated moderately well with the magnitude of changes in detection performance. The elevation of V1 activity by training likely results from an increase in the number of neurons responding to the trained stimulus or an increase in response gain.

Results and Discussion

Comparisons of single-unit data to animal and human performance suggest that detection of simple contrast patterns may depend relatively directly on the number and gain of responsive neurons in V1, with larger responses producing better detection performance [5, 6]. Recent results from fMRI have also linked contrast detection performance to the amplitude of V1 response [7, 8]. Accordingly, we hypothesized that training that improved detection performance would increase V1 response to the target.

We trained subjects to detect a low-contrast sinusoidal pattern and measured neural activity in V1 prior to

and after training with fMRI. Subjects practiced for more than 14,000 trials during more than 20 daily training sessions on a pattern that was oriented 45° clockwise from vertical and centered at 3.9° eccentricity. Behavioral thresholds and V1 response were measured for both the practiced and unpracticed control patterns, which included horizontal (principal) patterns at the trained location as well as principal and 45° (oblique) patterns at two other locations in the visual field (Figure 1). Measurements of neural response were taken from the portion of V1 that represented the part of the visual field covered by each stimulus. Average fMRI responses to principal and oblique patterns were calculated at all three locations.

Although subjects practiced detection of low-contrast patterns, during scanning they performed discrimination of high-contrast patterns. We chose this approach for two reasons. First, high-contrast patterns produce large stimulus-driven fMRI responses, which maximized our ability to measure potential differences in response as a function of stimulus orientation and training. Second, the use of discrimination allowed both the performance of subjects and the stimuli they viewed to be held constant in the pre- and post-training scanning sessions. Changing either the stimuli or subjects' performance between sessions would have introduced a confound in the design. Critically, the use of discrimination during scanning does not limit the interpretability of our results (see below).

Before training, subjects were reliably better able to detect the principal (horizontal) pattern than the oblique (45°) pattern at the two more-central stimulus locations (Figures 2 and 3). Similarly, V1 was reliably more responsive to the principal pattern than to the oblique pattern. Increased behavioral and neural sensitivity to principally oriented patterns relative to obliquely oriented ones has been termed the oblique effect and has been reported in many previous studies (e.g., [9–13]).

Training improved subjects' ability to detect the practiced pattern, with detection thresholds (contrast needed for 82% correct performance) improving by 17% on average (Figures 2 and 3). Learning was largely specific to the practiced stimulus. At the trained location, changes in thresholds were reliably smaller for the untrained orientation than for the trained one. Learning reduced the difference in response to the two orientations by roughly the same amount at the central and middle locations, but smaller effects of learning were seen at the peripheral location.

Training increased the response of V1 to the practiced pattern (Figures 2 and 3). Before learning, average signal amplitudes for the oblique pattern were 39% less than for the principal pattern; after learning, responses to the two patterns were close to equal. Because fMRI signal strength and signal-to-noise ratio can vary across cortical locations and scanning sessions, we quantified our results by comparing responses to the two orientations gathered under the same conditions. An *oblique index* was calculated for responses at each stimulus location

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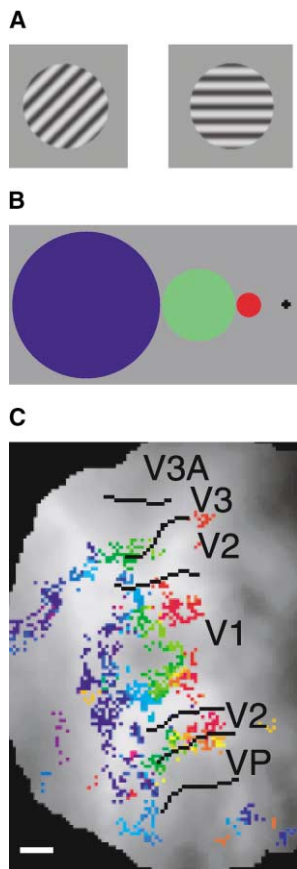


Figure 1. Methods

(A) Stimuli were sinusoidal grating patches oriented obliquely, at 45°, or horizontally (a principal orientation).
 (B) Stimuli were presented at one of three locations in the visual field and were scaled in both size and spatial frequency to account for cortical magnification (see Experimental Procedures).
 (C) A flattened representation of one subject's visual cortex, with responses to the localizer scan superimposed. Colors have been assigned to indicate the regions in cortex that are responsive to each stimulus location in correspondence with the colors used in (B). Colors were determined with the phase of response in a localizer scan (see Methods). The scale bar represents 1 cm.

in each scanning session by subtracting the fMRI response amplitudes for the two orientations and then dividing by the sum of these amplitudes. Positive indices reflect greater response to the principal than to the oblique stimulus, negative indices reflect the opposite, and indices near zero reflect equal responses. The oblique index measures relative responsiveness independently of changes across scanning sessions. Because different populations of neurons are likely responding to the two different orientations, this index does not relate directly to the orientation bandwidth of individual neurons.

Cortical changes were relatively specific to the trained orientation and produced a reliable decrease in the oblique index at the trained location (from 0.28 to -0.06, Figure 3). Cortical changes were also relatively specific to the trained location. There was a nonsignificant trend for the effects of learning to be smaller at the middle location than at the trained, central location, and reliably

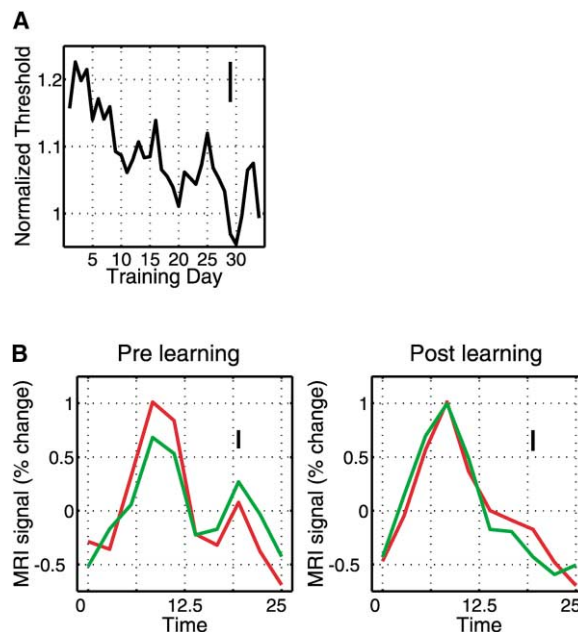


Figure 2. Behavioral and Cortical Effects of Learning

(A) Average learning curve shows decreasing behavioral thresholds for the trained oblique stimulus across days for six subjects. For normalization of learning curves, each subject's oblique thresholds were divided by that subject's threshold for the principal stimulus measured prior to learning. Because detection is better for the principal stimulus (raw principal thresholds are smaller than raw oblique thresholds), the normalized thresholds are greater than one. The vertical bar shows an average standard error of the mean.
 (B) Average fMRI responses to the oblique (green) and principal (red) stimulus before and after learning for five subjects. Data were averaged from pixels in V1 that responded to the trained location during the localizer scan. Bars indicate average standard error of the mean. Units are percent change from a baseline defined as the mean of the time course. Prior to learning, the oblique stimulus generated a weaker response in V1 than the principal stimulus. Learning abolished this difference.

smaller effects of learning were seen at the peripheral location.

The observed increases in V1 response correlated with the magnitude of the neural and perceptual learning effects (Figure 4). To facilitate comparison, we calculated a behavioral oblique index by subtracting detection thresholds for the two orientations and then dividing by the sum of these thresholds. Because smaller thresholds are associated with better performance, we subtracted the principal from the oblique thresholds to yield an index where greater values reflected better performance on the principal pattern. Figure 4 plots changes in the behavioral oblique index against changes in the fMRI oblique index (computed as above) across learning. The reliable correlation shows that larger increases in V1 response were indeed associated with larger increases in performance. Some contribution to the behavioral oblique effect does likely arise beyond V1, however; on average, learning equalized neural responses to the two stimuli at the trained location, whereas behavioral thresholds remained slightly different. Note further that the changes in the fMRI oblique index were larger in absolute terms than the changes in the behavioral

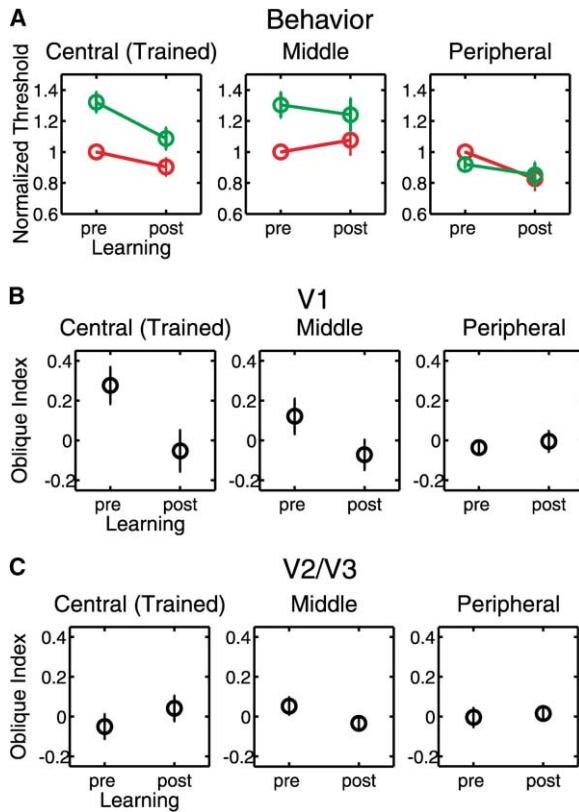


Figure 3. Quantified Effects of Learning

(A) Average behavioral thresholds for the oblique degree stimulus (green) and the principal stimulus (red) before and after learning for six subjects. Thresholds have been normalized relative to those for the horizontal stimulus prior to learning. Error bars represent \pm one standard error (between subjects). Training reduced thresholds by a larger amount for the trained (oblique) stimulus than for the untrained (principal) stimulus (18% versus 9.7%; $t(5) = 2.6$; $p < .025$; one-tailed probabilities reported for all tests) at the trained location. The spatial specificity of learning was measured with oblique indices calculated for each stimulus location (see text for details). For behavior, larger indices signify better performance on the principal stimulus than on the oblique stimulus; for fMRI response, larger indices signify higher amplitude responses to the principal stimulus than to the oblique stimulus. Changes in the behavioral oblique indices were smaller for the peripheral location than the for the trained locations [$t(2) = 7.4$; $p < .01$], but differences between the trained and middle locations did not reach significance.

(B) Average oblique indices calculated from the amplitudes of the fMRI responses in V1 of five subjects. At the central location, prior to learning, response amplitudes were larger to oblique stimuli, as indicated by a positive oblique index [$t(4) = 2.9$; $p < .025$]. After learning, the amplitude of the oblique index was reduced [$t(4) = 2.4$; $p < .05$], and responses to the two stimuli were close to equal, as indicated by an index near zero. Some effects of learning were seen at the middle location [$t(4) = 1.8$; $p < .1$], and less learning was seen at the peripheral location than at the central one [$t(4) = 2.8$; $p < .025$].

(C) Average oblique indices calculated from V2/V3. No consistent effects of learning were seen.

index. Given their different underlying scales, there is no reason to expect changes in fMRI response to map onto changes in threshold with a slope of unity.

In areas V2 and V3, learning produced little observable effect (Figure 3). Responses between the vertical and

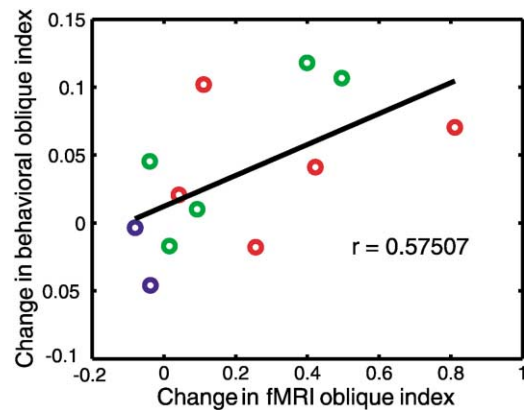


Figure 4. Correlation between Behavior and V1 Response

A reliable correlation [$t(10) = 2.2$; $p < .025$] was observed between changes in V1 oblique indices and changes in behavioral oblique indices across learning. Each point represents one stimulus location from one observer. Useful fMRI data were obtained from only five observers, and behavior was measured at the third eccentricity for only two of these observers, yielding a total of 12 points. Color indicates the visual-field location at which each data point was obtained, with red, green, and blue standing for the central, middle, and peripheral stimulus locations, respectively.

oblique stimuli were close to equal prior to learning and did not change reliably. These results suggest that the changes seen in V1 were not due to some global factor, such as arousal, that would increase signal throughout responding regions of visual cortex.

The amplitude of a secondary peak visible in the fMRI time course from the central location (Figure 2) decreased after training. The timing of this later peak matched the stimulus timing at the middle location and likely reflects neural response to that stimulus. This secondary response could be caused by receptive fields that span both stimuli, spatial blurring of the hemodynamic response, noise in the localizer scan, or eye movements during scanning. For example, subjects may have occasionally fixated the middle location, thus moving it to the central location. The reduction in secondary response with learning was not specific to the practiced orientation and so could be due to changes in any of these factors. Importantly, our measure of learning in the primary peak controlled for possible changes in factors such as these because the oblique index compared responses to the two orientations measured under the exact same conditions.

Contrast detection is likely to depend relatively directly upon the number and responsiveness of neurons that respond to a pattern [5–8], and so we expected training to increase the total response of V1 to the trained stimulus. The data reported here clearly indicate that practicing a detection task can boost this response.

Two types of neural change can explain our data. One possibility is that learning could have increased firing rates in the same neurons that responded to the trained stimulus prior to learning, by changing either the gain or the asymptotic firing rates of responding neurons. Alternatively, training could have shifted receptive fields to increase the number of neurons that respond to the practiced stimulus. Such changes occur in somatosen-

sory cortex, for example, where the number of neurons preferring input from a trained finger increases with practice [4]. In our task, neurons' preferred orientations may have shifted toward the trained stimulus. The observed changes in V1 could be produced locally or could result from feedback from higher cortical areas.

Studies of V1 with single-unit recording report different neural effects of learning than those observed here [14–16]. None of the studies reported increases in either the number or contrast gain of neurons that respond to the stimulus. Two studies nevertheless showed neural changes that can potentially account for the observed perceptual learning. In one, animals were trained to discriminate between two orientations, a task that may rely upon neurons that respond moderately to one of the orientations and less to the other orientation. Learning sharpened the orientation-tuning curves of such neurons by increasing the moderate responses to the more-preferred orientations, decreasing the responses to the less-preferred orientations, and thus amplifying a signal that could be used for discrimination [14] (but see [16]). Similar sharpening of tuning was seen in a position discrimination task [15].

The probable reason for difference between single-unit results and our results is the difference in the trained task. Our study likely boosted the total response to the trained stimulus because this response is used relatively directly in detection. Similarly, the single-unit studies found changes in neural signals that are likely responsible for behavior in the discrimination tasks the animals were performing. It remains possible, however, that the differences in methodologies (fMRI versus single units) could account for the differences in results.

Two prior imaging studies of perceptual learning in V1 also used discrimination tasks, and they yielded conflicting results. A PET study [17] found decreases in activity in early visual cortex after training, whereas an fMRI study [18] showed increases in V1 response. The tasks used in the two studies differed considerably, however, and the type of discrimination that is practiced could influence the amount and nature of plasticity seen in V1. Subtle differences in training or task may likewise explain differences in single-unit results [5, 7].

Our data do not show either an oblique effect or an effect of learning in areas V2 and V3. The former is in agreement with macaque V2 single-unit recordings, which failed to find reliably larger numbers of neurons tuned to principal orientations than to oblique ones [19]. Recent results from recordings in cats suggest that the oblique effect may be found only in simple cells [13], which are relatively scarce in primate V2 [19]. If V2 fails to show a neural effect, how then can a behavioral oblique effect for detection be observed? One possibility is that V2 neurons integrate and normalize V1 signals so that principal orientations produce more reliable, less noisy spike trains than do oblique orientations but that the average firing rates produced by the two types of stimuli do not differ. Another possibility is that only a relatively small subset of V2 neurons carries signals relevant for detection. Both accounts can explain why we did not observe an effect of learning in V2; neither changes in spike train reliability nor changes in a small population of neurons will be visible in the fMRI response.

Only two prior psychophysical studies have trained subjects in detecting gratings on a uniform field [20, 21]. These studies found slightly greater reductions in threshold—roughly 40% and 25%, respectively—than reported here, which may in part be due to learning during the extensive pretesting in our study (four 45 min sessions over 2 days). There remains some uncertainty over the specificity of learning with respect to orientation. Our data indicate that learning transfers relatively little from a trained oblique orientation to an untrained principal one. These results agree with one prior finding [20], but both prior reports show some transfer between a trained oblique orientation and an untrained orthogonal oblique orientation [20, 21]. Because we tested only one oblique orientation, we cannot determine the extent to which the learning observed here generalized to other oblique orientations.

Subjects in our study all trained on the same oblique orientation. Because the principal orientations, horizontal and vertical, are already overrepresented in V1 [10–13], it is possible that training them would produce different behavioral and neural results. Many of our subjects did show some transfer of learning to the principal orientation, however (Figure 3). The correlation we measured between changes in the neural and behavioral oblique indices suggests that learning at both orientations may be reflected in V1 response.

Although subjects practiced detection of low-contrast patterns, they performed discrimination of high-contrast patterns while fMRI measurements were made. Critically, the change in stimulus and task between training and scanning does not invalidate the interpretation of our results. This is because the relative responsiveness of neurons to different orientations (orientation tuning) has been shown to remain constant as contrast changes [22, 23]. Hence, if training caused a larger relative neural response to oblique patterns at threshold contrast levels, then the oblique patterns will produce a larger relative neural response at high-contrast levels. Additionally, changing tasks is not likely to change orientation tuning for the simple grating stimuli used here. Thus, the simplest interpretation of our results is that detection training strengthened neural response to the low-contrast oblique pattern, which in turn produced an increase in response while subjects were discriminating high-contrast oblique patterns.

Visual attention can have large effects on the fMRI response in primary visual cortex (e.g., [24–26]), but differences in attention are not likely to explain our results. An attentional explanation of our results would have to propose that subjects paid greater attention to the oblique stimuli than to the principal stimuli after training. Two patterns in our data make such a scenario unlikely. First, performance on the discrimination task during scanning did not reliably differ between sessions or conditions. Because behavior was neither at ceiling nor chance levels, differences in attention would be expected to produce differences in task performance; performance on the oblique stimulus should have been relatively superior after training. The nonsignificant trends in our data were in the opposite direction; in the pretraining scanning sessions subjects responded correctly on 75% of the principal discrimination trials

and 84% of the oblique discrimination trials at the central location. After training, subjects responded correctly on 80% of the principal trials and 79% of the oblique trials at the central location. Second, we saw no effect of training in V2. If our learning effects in V1 were due to changes in attention, then we should have observed substantial effects in extrastriate cortex, where attentional effects are generally larger (e.g., [27]).

Conclusions

Our findings, together with prior results, suggest that early visual cortex can reorganize in a variety of ways. Practicing orientation discrimination, for example, may lead to neural changes—a sharpening of orientation tuning—that strengthen the most useful signals for the task. Practicing detection can lead to changes—an increase in number or gain of responsive neurons—that strengthen the weak signals used to detect faint patterns. Cortex may be capable of enhancing precisely the neural signals that produce greatest improvement in task performance.

Experimental Procedures

Subjects

Six subjects participated in the experiment. fMRI data from one subject contained uncorrectable large artifacts due to head motion and so were excluded from analysis.

Stimuli

Subjects viewed contrast patterns centered at three locations in the visual field: 3.9°, 8.9°, and 20.1° eccentricity. Size and spatial frequency were scaled for cortical magnification, with patterns subtending 2.8°, 6.4°, and 14.6° of visual angle and all containing a spatial frequency of six cycles per stimulus. Only one pattern at a time was displayed. During fMRI scans, stimuli were displayed on a rear projection screen by an LCD projector. For psychophysics, subjects viewed displays on a calibrated monitor driven by a graphics card with 10 bits per gun.

Tasks

Subjects performed two-interval forced-choice detection and discrimination tasks while fixating a central point binocularly. Trials were 3 s long and consisted of two approximately 300 ms intervals separated by 1300 ms and an 1100 ms response period. In the detection task, subjects indicated which of the two intervals contained a stimulus, and the contrast of the stimulus varied under the control of a staircase procedure.

In the discrimination task, both intervals contained high contrast (95%) stimuli, and subjects indicated which of the two patterns was tilted more clockwise. One of the stimuli to be discriminated was oriented at the reference orientation (either 45° [oblique] or 0° [principal]), and the second was oriented at the reference orientation plus an increment in orientation (e.g., 45 + 5 = 50°). The size of the orientation increment varied under the control of a staircase procedure.

Psychophysical Paradigm

Before and after training, thresholds were measured for both detection and orientation discrimination by staircase procedures. Subjects performed separate blocks of trials of each task, eccentricity, and orientation in randomized order. For measuring perceptual thresholds, Weibull functions were fit to the data to give an estimate where performance was 82% correct. Posttraining data for the most eccentric stimulus was gathered for only three subjects.

During training, subjects practiced only detection of the oblique stimulus presented at the central location. Subjects trained in one or two sessions (25–40 min, 500–600 trials per day, mean of 16,600

total trials) on each of 29 ± 2 (standard deviation, s.d.) days on average, spread over an average time period of 53 ± 8 days.

fMRI Paradigm, Data Acquisition, and Analysis

During scanning, subjects performed two trial mini-blocks of the discrimination task (0 ms between trials) followed by 2.333 s of rest. The orientation increments for each subject were fixed with pretesting data (principal mean = 2.4 ± 1.2 (s.d.); oblique mean = 6.7 ± 1.6), and the reference orientations (either principal or oblique) alternated between mini-blocks. Successive trials were performed at the different locations in a fixed sequence (central, middle, peripheral, central...), yielding a 25 s cycle for a given stimulus location. Examination of average raw time courses revealed that the fixed trial order did not introduce baseline differences between conditional responses that affected the overall pattern of results. Subjects performed 36 mini-blocks of trials per fMRI scan (BOLD imaging at 3 Tesla, TR = 2.5, TE = 45, FA = 90, voxel size = 3.25 × 3.25 × 4 mm) and four or five scans per session.

V1 and other early visual areas were identified by standard techniques [28–31]. Active voxels in early visual areas were identified by a separate reference scan of high-contrast flickering checkerboard patterns identical in size to the sinusoidal patterns. Patterns were presented sequentially for 16.66 s each, yielding a phase-encoding of stimulus location. fMRI data were averaged separately from regions of interest (ROIs) comprising voxels that responded (correlation greater than 0.25) to each pattern during the reference scan (as determined by phase of response). Regions of interest in V1 averaged 476, 421, and 761 mm³ at the central, middle, and peripheral locations. We were unable to separate responses from V2 and V3 because our stimuli were presented close to the horizontal meridian, which is represented at the border between these areas, and so they were treated as a single ROI. We also could not measure responses in more anterior visual areas because increasing receptive field sizes greatly reduced signal from the reference scan.

Average fMRI signals were computed for principal and oblique mini-blocks for each ROI across either 24 or 30 repetitions per condition. Prior to averaging, the fMRI time course for each voxel was converted to a percent change score by first subtracting and then dividing by the mean. Response amplitudes were measured as the height of a model hemodynamic response (computed by convolving a gamma function [32] with the stimulus time course) that best fit the data. Separate delay parameters in the model response were allowed for each condition and each subject.

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