Enhanced attentional gain as a mechanism for generalized perceptual learning in human visual cortex

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Enhanced attentional gain as a mechanism for generalized perceptual learning in human visual cortex. J Neurophysiol 112: 1217–1227, 2014. First published June 11, 2014; doi:10.1152/jn.00353.2014.—Learning to better discriminate a specific visual feature (i.e., a specific orientation in a specific region of space) has been associated with plasticity in early visual areas (sensory modulation) and with improvements in the transmission of sensory information from early visual areas to downstream sensorimotor and decision regions (enhanced readout). However, in many real-world scenarios that require perceptual expertise, observers need to efficiently process numerous exemplars from a broad stimulus class as opposed to just a single stimulus feature. Some previous data suggest that perceptual learning leads to highly specific neural modulations that support the discrimination of specific trained features. However, the extent to which perceptual learning acts to improve the discriminability of a broad class of stimuli via the modulation of sensory responses in human visual cortex remains largely unknown. Here, we used functional MRI and a multivariate analysis method to reconstruct orientation-selective response profiles based on activation patterns in the early visual cortex before and after subjects learned to discriminate small offsets in a set of grating stimuli that were rendered in one of nine possible orientations. Behavioral performance improved across 10 training sessions, and there was a training-related increase in the amplitude of orientation-selective response profiles in V1, V2, and V3 when orientation was task relevant compared with when it was task irrelevant. These results suggest that generalized perceptual learning can lead to modified responses in the early visual cortex in a manner that is suitable for supporting improved discriminability of stimuli drawn from a large set of exemplars.

PERCEPTUAL LEARNING (PL) REFERS TO AN IMPROVED ABILITY TO DETECT OR DISCRIMINATE A SENSORY STIMULUS AFTER REPEATED EXPOSURE (Gibson 1963, 1969). This behavioral improvement is thought to be supported by at least two neural mechanisms: an increase in the fidelity of early sensory responses (sensory modulation account) and/or an increase in the efficiency with which early sensory information is relayed to, or “read out” by, downstream decision mechanisms (enhanced readout account). Consistent with the sensory modulation account, learning for a specific feature can enhance the gain of informative sensory signals (Zohary et al. 1994; Gilbert et al. 2001; Schoups et al. 2001; Furmanski et al. 2004; Yang and Maunsell 2004; Bao et al. 2010; Jehee et al. 2012) and reduce correlated noise shared between visually responsive neurons (Adab and Vogels 2011; Beijjanki et al. 2011; Gu et al. 2011). Conversely, readout models can explain improved perceptual performance without the need to invoke learning-related changes in the fidelity of responses in early sensory areas (Dosher and Lu 1999, 2007, 2009; Lu and Dosher 1999; Petrov et al. 2005; Lu et al. 2010, 2011; Huang et al. 2012) and empirical data suggest that training can modify the degree to which informative sensory neurons are weighted during decisionmaking, particularly when a large set of training stimuli are employed [i.e., the trained stimuli change from session to session (Law and Gold 2008, 2009, 2010; Gold et al. 2010)].

However, most prior investigations that documented changes in early sensory modulation trained subjects to discriminate a single feature value (often in a single location), so the degree to which sensory modulation can support PL across multiple stimulus exemplars is largely unknown. This is an important question, as many real-world instances of PL require identifying unique members from a broad class of possible features: a radiologist must find a small fracture irrespective of its precise location or its exact orientation, and a baggage screener at an airport must detect potential weapons of all shapes and sizes hidden in a piece of luggage. Intuitively, this more general form of PL might be supported primarily by changes in the readout of unmodified sensory signals (e.g., Law and Gold 2008), as any plasticity in sensory areas that facilitates the processing of one specific exemplar might interfere with the processing of other exemplars (Schoups et al. 2001; Fahle 2004, 2009). On the other hand, it is possible that learning modulates early sensory responses in a more flexible manner that facilitates the processing of all stimuli from the trained set of exemplars, perhaps by enhancing the overall gain of feature-selective responses in early visual areas. Here, we tested this latter hypothesis in human subjects using functional magnetic resonance imaging (fMRI) and a multivariate analysis technique that assesses how PL modifies the characteristics of population-level orientation-selective tuning profiles in human visual cortex.

METHODS

Subjects. Thirteen subjects (7 males and 6 females) between the ages of 18 and 28 (M = 21.5, SD = 2.8) were recruited from the University of California, San Diego to participate in the experiment, and all gave written informed consent in accordance with the Institutional Review Board at University of California, San Diego. Of these 13 subjects, 5 were excluded from analysis: 1 did not complete both scanning sessions, 2 could not do the task for unknown reasons (with final day orientation offsets of 24 and 40°, which were ≈3–10 times larger than the other subjects), and 2 showed significant motion artifacts (i.e., multiple abrupt translations of 5 mm or more in both scanning sessions). Subjects performed a brief 20-min familiarization session before the initial scanning session, a 2-h pretraining fMRI...
scan, ten 1-h behavioral training sessions in the laboratory, and a final 2-h posttraining fMRI scan. Subjects were compensated $100/h for the training sessions and $20/h for the scan sessions.

**Stimulus and task.** All stimuli were created using MATLAB (v.7.8; The Math Works, Natick, MA) with the Psychophysics Toolbox (v.3; Brainard 1997; Pelli 1997). The physical properties of the stimulus display were identical across two attention conditions: (1) attend to the orientation of a grating stimulus (attend-orientation) and (2) attend to a central rapid serial visual presentation (RSVP) stream of letters (attend-RSVP). Each trial started with a 200-ms fixation interval, followed by a peripheral circular square-wave grating and a centrally presented RSVP stream (Fig. 1). The grating had a radius of a 10° visual angle and a spatial frequency of 0.5 cycles per degree and flickered at a rate of 5 Hz. The inner blank aperture around fixation extended to a 2° visual angle. The orientation of the grating was pseudorandomly selected on each trial from a set of nine possible orientations that were evenly distributed across 180° of orientation space; ±3° of orientation jitter was randomly added to the first grating on each trial to ensure that subjects could not make their judgment with respect to a fixed orientation. The spatial phase of each of the gratings was also randomly determined on each trial to ensure that measured signals were related to orientation and not to specific luminance patterns on the display screen. After 2,080 ms, the grating was removed from the screen for 400 ms, and then a second flickering grating was presented for an additional 2,000 ms. On attend-orientation blocks, the subject’s task was to press one button if the second stimulus was rotated clockwise from the first stimulus, and another button if it was rotated counterclockwise from the first stimulus (buttons were pressed with the first 2 fingers of the right hand). The RSVP stream appeared within the inner blank aperture of the grating, with each letter subtending at a 1.2° visual angle. The letter stream was presented during the same temporal epochs in which the oriented gratings were presented (i.e., 2,000 ms on, 400 ms off, 2,000 ms on).

![Fig. 1. Schematic of the experimental paradigm. In both task types (attend-orientation/attend-RSVP), subjects viewed a 2-s presentation of a annular square-wave grating with a rapid serial visual presentation (RSVP) letter stream in the center, followed by a 400-ms blank interstimulus interval (ISI), and then another 2-s exposure to a grating and a central RSVP stream. While visible, the gratings flickered at 5 Hz to drive a strong visual response (and the phase of the grating’s spatial frequency was randomly selected on each finger). On attend-orientation blocks, subjects indicated whether the second grating was rotated clockwise or counterclockwise from the first grating. On attend-RSVP blocks, subjects monitored the RSVP stream for a target letter (either “X” or “Y”) and indicated whether the target letter in the second stream matched (i.e., “X” or “Y”) or mismatched (i.e., “X” followed by a “Y” or vice versa) the target letter in the first stream. Subjects responded via a manual button press with either their index finger (to indicate a clockwise rotation of the gratings or a mismatch between target letters) or their middle finger (to indicate a clockwise, rotation of the gratings or a mismatch between target letters).](http://jn.physiology.org/)

Either an “X” or a “Y” was presented within each epoch of RSVP, and on attend-RSVP blocks the subject’s task was to press one button if the target letters matched (i.e., “X” or “Y”) and another button if the target letters did not match. Subjects had 2,000 ms to respond after the stimuli were removed from the screen, and this response window also served as the intertrial interval (ITI).

At the beginning of each training session, the clockwise or counterclockwise rotational offset between the first and second gratings was set to 30°, and performance was adjusted using the QUEST algorithm (Watson and Pelli 1983). The orientation offset required to achieve 75% accuracy was taken as the threshold for each session, and learning was operationalized as the change in the angular offset between the first and second gratings that was required to achieve threshold accuracy during each testing session. The exposure duration of each letter in the RSVP stream was manually adjusted to achieve ~75% accuracy to ensure that the task remained equally challenging across training sessions.

**Training regimen.** Before the initial scan session, subjects performed 4 blocks of 36 trials of the task (2 blocks of each of the attend-orientation and attend-RSVP conditions) to familiarize them with the task. After the initial scan session, subjects completed ten 1-h training sessions. During each training session, subjects performed four blocks of the attend-orientation condition and four blocks of the attend-RSVP condition, with each condition alternating on a block-by-block basis. Auditory feedback (short beeps, 100-ms duration) was provided to indicate correct and incorrect responses during the familiarization and training phases but not during either scan session. After the 10th training session, subjects completed the second scan session.

**fMRI sessions.** Subjects performed eight blocks of the behavioral task in each of the two scan sessions, and each block lasted 5 min. Eight null trials were randomly interleaved with 36 task trials in each block. For the first scan session, the offset between the two presentations of the grating was based on the staircased offset from the familiarization session (M = 8.3°, SE = 4.7°) and was manually adjusted at the end of each block based on subject performance to maintain consistent performance across runs (M = 8.1°, SE = 0.95°). The letter exposure duration was also based on the exposure duration from the familiarization session (M = 157.1 ms, SE = 6.1 ms), but this number was decreased slightly in the scanner (M = 140.7 ms, SE = 9.5 ms), due to relatively high accuracy on this task during the pretuning session. For the second scan session, the orientation offset was based on the final training session (M = 2.9°, SE = 0.64°) and again was manually adjusted at the end of each block to maintain consistent performance across runs (M = 5.1°, SE = 0.33°). The letter exposure duration was also based on the last training session (M = 33.0 ms, SE = 0.0 ms), and this number was also manually adjusted to maintain consistent performance (M = 85.4 ms, SE = 5.0 ms).

**Functional localizer scans.** Two 6.6-min functional localizer scans were run in each scan session to independently identify voxels in retinotopically organized early visual areas that responded to stimuli in the spatial location occupied by the visual stimulus in the main task. On each trial, a contrast-reversing checkerboard stimulus (spatial frequency = 1 cycle/°, temporal frequency = 8 cycles/s) was presented in the center of the screen for 10 s. On half of the 16 trials, the radius of the stimulus was a 5° visual angle and on the other half the radius of the stimulus was a 1° visual angle (matching the size of the stimulus used in the main learning experiment). Subjects were instructed to press a button whenever the contrast of the flickering stimulus dimmed slightly. Contrast-dimming target events occurred four times per trial, and each dimming lasted for 66.7 ms. The occurrence of each target was determined pseudorandomly, with the constraint that the target appeared at least 1 s after stimulus onset and 1 s before stimulus offset, and each target was separated from the previous one by at least 1 s. Trials were separated by a 10-s ITI.

**Retinotopic mapping.** A standard meridian mapping procedure was used to identify visual areas V1, V2v/V2d, and V3/V3d. Subjects passively viewed a contrast-reversing checkerboard stimulus flickering at 8 Hz and...
covering 60° of polar angle and that alternated every 20 s between the horizontal and vertical meridians (Engel et al. 1994; Sereno et al. 1995). A standard general linear model (GLM) with regressors corresponding to epochs of vertical meridian and horizontal meridian stimulation was used to identify voxels in the visual cortex that responded to each respective region of the visual field. Each regressor was generated by convolving a boxcar model of each stimulus time series (“0” if no stimulus, “1” if stimulus present) with a standard difference-of-two gamma function model (time to peak of positive response: 5 s; time to peak of negative response: 15 s; ratio of positive and negative responses: 6; positive and negative response dispersion: 1). The retinotopic mapping data were then projected onto a computationally inflated rendering of each subjects’ gray/white matter boundary to facilitate the identification of the horizontal and vertical meridians to define each cortical area. Because we used a large central stimulus, voxels in ventral and dorsal aspects of V2 and V3 were combined.

fMRI data acquisition and preprocessing. Scanning was performed using a 3T GE MR750 MRI scanner with an eight-channel head coil at the University of California, San Diego’s Keck Center for Functional MRI. Anatomical images were collected using a T1-weighted (TR/TE = 11/3.3 ms, TI = 1,100 ms, 172 slices, flip angle = 18°). Functional images were collected using a gradient echo EPI pulse sequence with 35 slightly oblique slices, which covered the whole brain. The slices were collected in ascending interleaved order and were 3-mm thick (TR = 2,000 ms, TE = 30 ms, flip angle = 90°, image matrix = 64 (AP) × 64 (RL), with FOV = 192 mm (AP) × 192 mm (RL), voxel size = 3 × 3 × 3 mm). All EPI images were slice-time corrected, motion-corrected (both within and between scans), and high-pass filtered (3 cycles/run). BrainVoyager QX (v2.3; Brain Innovation, Maastricht, The Netherlands) was used to perform the data analysis in conjunction with custom analysis scripts written in MATLAB (version 7.11.0584; The Math Works).

Analysis of functional localizer data. Data from the functional localizer scans were analyzed using a GLM that contained separate regressors marking the temporal interval in which each of the two stimulus types was presented (small checkerboard and large checkerboard). Each regressor was generated by convolving a boxcar model of the stimulus time series (“0” if no stimulus, “1” if stimulus) with a standard difference-of-two gamma function model (time to peak of positive response: 5 s; time to peak of negative response: 15 s; ratio of positive and negative responses: 6; positive and negative response dispersion: 1). A contrast was then performed to identify voxels that responded more to the large 10° checkerboard compared with the small 5° checkerboard; this contrast was intended to exclude voxels that respond strongly to the location of the central RSVP stream. Voxels within each of the visual areas were included in subsequent analyses if they passed a threshold of P < 0.05, after using BrainVoyager’s false discovery rate algorithm to correct for multiple comparisons.

Estimating trial-by-trial blood oxygen level-dependent responses on attention scans. Before estimating the trial-by-trial magnitude of the blood oxygen level-dependent (BOLD) response during the main attention task, we first estimated the shape of the hemodynamic response function (HRF) separately for each visual area in each subject. This subject- and area-specific fitting was done because the shape of the HRF can vary substantially across subjects and brain regions (Zarahn et al. 1997; Gonzalez-Castillo et al. 2012). Data were averaged across all trials in the main scans, and the mean stimulus-locked HRF was computed separately for each visual area in each subject, with voxels in the visual cortex that corresponded to each respective region (Dale 1999). We then used a gradient descent algorithm implemented in MATLAB to fit each HRF estimate using a standard difference-of-two gamma function model with time to peak, onset time, and the ratio of positive and negative components as free parameters (using the same seed parameters listed in Analysis of functional localizer data). The parameters that yielded the best fit were used to produce a custom HRF model for each visual area in each subject. We then created a design matrix with a boxcar model of the onset/offset time of each 4.4-s stimulus epoch on each trial within a scan, yielding 36 regressors of interest (4 instances of each of the 9 orientations) along with 1 additional regressor as a constant term. Each boxcar regressor model was then convolved with the custom HRF estimate for that subject, and a GLM was used to estimate the relative amplitude of the BOLD response on each trial. This estimate of response amplitude one each trial in each voxel was then used as input to the orientation encoding model described below.

Estimating orientation-selective BOLD tuning profiles using a forward encoding model. Forward encoding models adopt a set of prior assumptions about the important features or stimulus labels that can be distinguished using hemodynamic signals within a region of interest (ROI) (Brouwer and Heeger 2009, 2011; Dumoulin and Wandell 2008; Gourtzelidis et al. 2005; Kay and Gallant 2009; Kay et al. 2008; Mitchell et al. 2008; Naselaris et al. 2009; Schönwiesner and Zatorre 2009; Scolari, et al. 2012; Thirion et al. 2006; reviewed in Naselaris et al. 2011; Serences and Saproo 2012). The features or labels in the model are then used to predict the pattern of BOLD responses. Unlike multivoxel pattern analysis (MVPA) decoding techniques, this approach allows us to quantify changes in the shape of orientation-population response profiles that are related to PL. This technique thus complements MVPA approaches, as MVPA provides an index of how much overall information is encoded in a pattern of responses and how that level of information changes as a result of PL (or other experimental manipulations: see Serences and Saproo 2012). However, a general increase in the information content of a response pattern might be supported by several different types of modulation (i.e., a decrease in the bandwidth of orientation-selective population tuning profiles, an increase in gain of orientation-selective population tuning profiles, etc.). Thus, by directly reconstructing population tuning profiles using an a priori encoding model, we can quantify the modulatory patterns that occurred as a result of generalized PL.

Here, we used a forward model adapted from Brouwer and Heeger (2009, 2011) to estimate the response across a series of orientation channels as a function of PL and the focus of attention. The model assumes that the BOLD response in a given voxel reflects the pooled activity across a large population of orientation-selective neurons and that the distribution of neural tuning preference is biased within a given voxel either due to large-scale feature maps (Freeman et al. 2011) or to subvoxel anisotropies in cortical columns (Kamitani and Tong 2005; Swisher et al. 2010). In either case, BOLD responses measured from many voxels in early visual cortex exhibit a modest but robust orientation preference (Haynes and Rees 2005; Kamitani and Tong 2005; Serences et al. 2009; Freeman et al. 2011).

For each subject and scan session, we first split the data into two sets (training and test sets), using a hold-one-out cross-validation method. Adopting the terminology and formulations of Brouwer and Heeger (2009, 2011) for consistency, let m be the number of voxels in a given visual area, n₁ be the number of observations (trials) in the training set, n₂ be the number of trials in the test set, and k be the number of hypothetical orientation channels. Let Bⱼ (m × n₁ matrix) be the training set, and B₂ (m × n₂ matrix) be the test set. The training data in B₁ were then mapped onto the matrix of hypothetical channel outputs (C₁, k × n) by the weight matrix (W; m × k) that was estimated using a linear model of the form:

\[ B₁ = WC₁ \]  

where the ordinary least-squares estimate of W is computed as:

\[ \hat{W} = B₁C₁(G₁C₁)⁻¹ \]  

The channel responses (C₂, k × n₂) were then estimated for the test data (B₂) using the weights estimated in Eq. 2:

\[ \hat{C}_2 = (\hat{W}^TW)^{-1}\hat{W}^TB_2 \]  

Equations 1 and 2 are similar to a traditional univariate GLM in that each voxel gets a weight for each feature in the model (in this case, 1...
weight for each orientation channel). Equation 3 then estimates channel responses on each trial based on the estimated weights assigned to each voxel and the vector of responses observed across all voxels on a given trial in the test set.

The construction of the basis set matrix C has a large impact on the resulting channel response estimates. In the present experiment, we used a half-sinusoidal function that was raised to the 5th power to emulate the approximate shape of single-unit tuning functions in V1, where the average 1/sqrt(2) half-bandwidth of orientation tuned cells is \textasciitranslation{\textdegree} 20° (Schiller et al. 1976; Ringach et al. 2002; Gur et al. 2005). This function was then replicated six times, with the six copies evenly distributed across orientation space. The power of the sinusoidal function necessitated the use of at least six copies to adequately cover orientation space (Freeman and Adelson 1991). While we selected the shape of the basis function based on existing physiology studies, all results that we report are robust to reasonable variations in this value (i.e., raising the half-sinusoid to the 5th, 6th, 7th, or 8th power, all of which are reasonable choices based the large range of single-unit bandwidths observed in visual areas). The analysis described above was then repeated with the center position of each of the six basis functions shifted across all 180° of orientation space in 1° increments to generate channel tuning functions with 1° resolution (which ultimately produced a 180° tuning function). Note that because of overlap between adjacent basis functions, each point along these 180-point tuning curves was not independent from neighboring points. However, this approach was adopted to maximize the smoothness of the tuning functions, which in turn facilitates quantifying the amplitude, bandwidth, and baseline level using the model fitting approach described below. Last, the 180-point channel response function estimated on each trial was circularly shifted so that the channel matching the orientation of the stimulus on that trial was positioned in the center of the tuning curve, thereby aligning all channel response profiles to a common stimulus-centered reference frame (which is plotted as 0° on the x-axis by convention, see Figs. 5–6). The channel responses for each subject were then averaged across subjects within each scanning session so that group channel response functions for the different attention and training conditions could be compared.

Quantifying channel responses by fitting a von Mises function. After the channel responses were recentered to a common reference frame, data from each subject and each condition (attend-orientation/attend-RSVP, pretraining/posttraining) were independently fit with a von Mises function:

\[ f(\theta) = ae^{[\cos(\theta-\mu)] - 1} + b \] (4)

with amplitude \(a\), mean \(\mu\), bandwidth \(\sigma\), and baseline \(b\) as independent free parameters that reflect distinct attributes of the function. The amplitude was restricted to a range from 0 and 2, the mean was restricted to a range from 60 and 120°, the bandwidth was restricted to a range between 0 and 8, and the baseline was restricted to a range from −3 and 3. The von Mises function (Eq. 4) was then fit to the data from each subject 150 times using randomly chosen initial seed values for each parameter on each iteration (across the range of allowable values) to ensure that the fitting algorithm did not settle in a local minimum. The set of parameters for each subject that yielded the lowest root mean squared error across the 150 iterations were then used in subsequent analyses.

RESULTS

Behavior during training sessions outside of scanner. The staircasing procedure did not converge for one subject during the first of their 10 behavioral training sessions, rendering data from session 1 highly variable (that subject had an orientation offset of 22.2°, where the mean across all other subjects was 4.7°). Therefore, statistical comparisons of the behavioral data were performed excluding this subject (although the size of the learning effect only increases if this subject is included, and their offsets during sessions 2-10 were stable and showed learning effects). The angular offset between the gratings needed to perform the task at criterion was steadily reduced across training sessions [see Fig. 2A; one-way repeated-measures ANOVA, \(F(9,54) = 2.18, P = 0.038\)], and there was a significant decrease in the average orientation offset between sessions 1 (4.7°) and session 10 [3.0°; paired t-test, \(t(6) = 3.4150, P = 0.014\)]. Response time did not significantly change across sessions 1-10 in the attend-orientation task [one-way repeated-measures ANOVA, \(F(9,54) = 0.48, P = 0.88\)]. Accuracy also did not significantly change across sessions 1-10 [see Fig. 2B; one-way repeated-measures ANOVA, \(F(9,54) = 0.8, P = 0.62\)], suggesting that staircasing was successful in maintaining a criterion level of accuracy.

Observers also improved in the attend-RSVP condition, such that the exposure duration of each letter in the RSVP stream

![Fig. 2. Behavioral performance for training sessions outside of the scanner. A: average orientation offset in degrees between the 2 gratings during each of the 10 behavioral training sessions (at a fixed accuracy threshold, see B). Note that for 1 subject, the staircasing procedure did not converge, leading to an overinflated estimate of their orientation offset on session 1; hence, all statistical analyses were performed excluding this subject (and data from that subject are excluded from this plot as well, see main text for more details). B: accuracy on the attend-orientation condition was maintained at a fixed rate across all behavioral testing sessions. C: average letter exposure duration in ms/letter across each of the 10 behavioral training sessions. D: accuracy on the attend-RSVP condition decreased across training sessions (see text for more details). All error bars \(\pm 1\text{SE}. *P < 0.05\), significance across sessions.](http://jn.physiology.org/)

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steadily decreased across the 10 training sessions [see Fig. 2C; one-way repeated-measures ANOVA, \( F(9,54) = 22.89, P = 0.0002 \)]. The average letter exposure duration also significantly decreased from 128.57 ms/letter during session 1 to 33.33 ms/letter during session 10 [paired t-test, \( t(6) = 8.40, P = 0.0002 \)]. However, accuracy also changed across the 10 sessions in the RSVP task [see Fig. 2D; one-way repeated-measures ANOVA, \( F(9,54) = 5.08, P = 0.0001 \)], suggesting that the reduction in exposure duration across sessions is not a perfect indicator of the amount of learning that occurred in the RSVP task (although this was not an issue when comparing pre- and posttraining behavioral performance in the scanner as all comparisons were carried out within session, see below).

Response times for the attend-RSVP condition did not significantly change across training sessions [one-way repeated-measures ANOVA, \( F(9,54) = 0.82, P = 0.6 \)].

**Behavior in the scanner.** In the scanner, the average orientation offset was 8.1° (SE = 0.95°) in the pretraining scan session and 5.1° (SE = 0.33°) in the posttraining scan session [Fig. 3A; paired t-test, \( t(7) = 3.84, P = 0.006 \)]. For the RSVP task, the pretraining letter presentation speed was 140.63 ms/letter (SE = 9.5 ms/letter) and the posttraining letter presentation speed was 85.42 ms/letter [SE = 5.0 ms/letter; Fig. 3C; paired t-test, \( t(7) = 6.33, P = 0.0004 \)]. We speculate that the slightly elevated orientation offsets and letter exposure durations in the scanner, compared with outside the scanner, were due to the lower quality visual display in the scanner. Accuracy on attend-orientation trials was slightly lower during the posttraining scan session compared with the pretraining session [see Fig. 3B; orientation task: 91% pretraining SE = 1%, 88% posttraining SE = 1%, paired t-test, \( t(7) = 2.78, P = 0.03 \)]. However, this small change in accuracy was not a major cause of the observed learning effects, as four subjects had balanced accuracy across pre- and posttraining scan sessions and they all showed at least 4° improvement with training. Accuracy in the attend-RSVP condition did not significantly differ across scan sessions [see Fig. 3D; letter task: 89% pretraining (SE = 2%) and 88% posttraining [SE = 2%, repeated-measures t-test, \( t(7) = 0.8769, P = 0.4 \)]].

**fMRI results.** First, we computed the mean univariate HRF for each attention condition based on the z-scored BOLD time series averaged across all voxels in each ROI (see METHODS; Fig. 4). As all three areas showed a similar pattern of responses, we performed statistics on the data averaged across V1, V2, and V3 (compare panels in Fig. 4). A three-way repeated-measures ANOVA with time (0–24 s), attention condition, and training (pre- vs. posttraining) revealed a main effect of time \([F(12,84) = 41.13, P < 0.0001]\), a main effect of attention condition \([F(1,7) = 36.91, P = 0.0005]\), and an interaction between time and attention \([F(12,84) = 12.24, P < 0.0001]\). However, there was no main effect of training \([F(1,7) = 0.11, P = 0.74]\) and no interaction between training and time \([F(12,84) = 7.99, P = 0.65]\) or training and attention condition \([F(1,7) = 2.91, P = 0.133]\). Overall, this pattern suggests that the HRFs were significantly modulated by attention but not by learning.

We then used an encoding model (see METHODS) to determine how learning modulated orientation-selective response profiles in V1, V2, and V3. Across both scan sessions and attention conditions, the averaged orientation-selective response profiles peaked at the target orientation and fell off in a Gaussian-like manner (see Figs. 5 and 6). We fit the tuning curve for each subject with a von Misses function and submitted the best fitting parameters to a three-way repeated-measures ANOVA with factors for attention condition (attend-orientation vs. attend-RSVP), training (scan 1 vs. scan 2), and visual area (V1, V2, V3). There was no main effect of visual area and no three-way interaction among visual area, attention condition, and training condition for any of the fit parameters (amplitude, bandwidth, baseline, or mean, see Table 1 for all statistics). This suggests that all areas showed a similar pattern of modulation across task manipulations (see Figs. 6 and 7 for data from individual visual areas). As a result, we hereafter focus our statistical analysis on the von Misses parameters fit to tuning functions that were computed after combining all voxels from V1-V3. Because the size of the orientation offset differed across pre- and posttraining scan sessions, a comparison between pre- and posttraining within each attention condition...
could not be directly assessed due to the sensory differences in the display. Thus we focused on evaluating a two-way repeated-measures ANOVA with attention condition and training as factors to compare with the magnitude of attention effects during pre- and posttraining sessions as our main marker of PL. The ANOVA revealed a significant overall main-effect of attention condition on the amplitude of the orientation-selective tuning profiles, such that the amplitude in the attend-orientation condition was higher than the amplitude in the attend-RSVP condition [collapsed across scanning sessions; Fig. 5, A and B; \( F(1,7) = 10.03, P = 0.015 \)]. In addition, there was a significant interaction between attention condition and training on tuning function amplitude, indicating that the magnitude of the attentional modulation (i.e., attend-orientation vs. attend-RSVP) increased with training [Fig. 5, C; \( F(1,7) = 7.98, P = 0.025 \)]. This interaction was driven by a significant difference between response amplitudes in the attend-orientation and attend-RSVP conditions posttraining but not pretraining \([t(7) = 3.5, P < 0.01 \text{ and } t(7) = 1.25, P = 0.25, \text{ respectively} \)]. Finally, there was an overall main effect of
attention condition on the baseline parameter, such that baseline estimates were higher in the attend-RSVP condition than the attend-orientation condition \[F(1,7) = 7.84, P = 0.026\]. No learning-related changes in any of the other parameters were observed.

**DISCUSSION**

Learning to better discriminate a specific stimulus feature has been associated with enhanced sensory responses in early visual cortex (Gilbert et al. 2001; Schoups et al. 2001; Furmanski et al. 2004; Yang and Maunsell 2004; Jehee et al. 2012) and with the improved readout of sensory information by downstream sensorimotor and decision mechanisms (Dosher and Lu 1998, 2009; Ghose et al. 2002; Law and Gold 2008, 2009, 2010; Xiao et al. 2008; Zhang et al. 2010b, 2013; Gold et al. 2010; Lu et al. 2011; Huang et al. 2012). However, little is known about how these mechanisms support PL in situations where observers must learn to make difficult discriminations between stimuli that are drawn from a large set of exemplars. Indeed, modified early sensory responses that are highly selective for supporting the discrimination of a specific feature might be predicted to impair the discriminability of other stimuli (e.g., Schoups et al. 2001; Fahle 2004, 2009). However, here we show that generalized PL leads to an enhancement of feature-selective attentional modulations in early visual cortex, supporting a version of the sensory modulation account of generalized PL.

Even though our data support a sensory modulation account of generalized PL, they do not speak to the possibility of additional contributions due to changes in the efficiency of sensory readout. Indeed, sensory modulation and changes in the efficiency of readout are not mutually exclusive. For example, Law and Gold (2008) trained subjects using a large stimulus set and their data provide support for enhanced readout in the absence of changes in early sensory responses in motion selective area MT. Their task involved discriminating stimuli moving in one of two directions, where the exact direction and location of the motion stimulus were changed on a session-by-session basis to optimize the response of cells in MT and the lateral intraparietal area (LIP). Law and Gold did not observe training-related changes in MT, an area that represents the quality of motion-evoked sensory signals. Instead, they found an increase in motion-driven responses in LIP, where cells are thought to play a role in the “readout” (or sensorimotor transformation) of sensory signals that are generated in MT. However, there are several differences between our study and theirs that might contribute to the differences that we observe. First, we used fMRI to assess the response profile across orientation channels tuned to all stimulus features (the entire range from 0 to 180°) whereas Law and Gold just assessed the activity of cells that were selectively tuned to the trained stimulus feature (or to the antipreferred feature). Thus we mapped out the full tuning profile and they mapped two points along this function. This could be a key difference, as our results suggest that the overall amplitude increase in fMRI-based orientation tuning profiles is due to a combination of factors.

Table 1. Statistical comparisons for each fit parameter across conditions and visual areas

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Error</th>
<th>F Statistic</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vis Area</td>
<td>(2, 14)</td>
<td>2.587</td>
<td>0.1107</td>
</tr>
<tr>
<td>Day</td>
<td>(1, 7)</td>
<td>0.009</td>
<td>0.9273</td>
</tr>
<tr>
<td>Attn Cond</td>
<td>(1, 7)</td>
<td>10.025</td>
<td>0.0158</td>
</tr>
<tr>
<td>Vis × Day</td>
<td>(2, 14)</td>
<td>0.711</td>
<td>0.5082</td>
</tr>
<tr>
<td>Vis × Attn</td>
<td>(2, 14)</td>
<td>0.241</td>
<td>0.7888</td>
</tr>
<tr>
<td>Day × Attn</td>
<td>(1, 7)</td>
<td>7.984</td>
<td>0.0256</td>
</tr>
<tr>
<td>Vis × Day × Attn</td>
<td>(2, 14)</td>
<td>2.903</td>
<td>0.0882</td>
</tr>
<tr>
<td>Baseline Vis Area</td>
<td>(2, 14)</td>
<td>3.346</td>
<td>0.0695</td>
</tr>
<tr>
<td>Day</td>
<td>(1, 7)</td>
<td>0.199</td>
<td>0.6687</td>
</tr>
<tr>
<td>Attn Cond</td>
<td>(1, 7)</td>
<td>7.84</td>
<td>0.0265</td>
</tr>
<tr>
<td>Vis × Day</td>
<td>(2, 14)</td>
<td>0.43</td>
<td>0.6591</td>
</tr>
<tr>
<td>Vis × Attn</td>
<td>(2, 14)</td>
<td>3.113</td>
<td>0.0761</td>
</tr>
<tr>
<td>Day × Attn</td>
<td>(1, 7)</td>
<td>4.121</td>
<td>0.0819</td>
</tr>
<tr>
<td>Vis × Day × Attn</td>
<td>(2, 14)</td>
<td>0.969</td>
<td>0.4037</td>
</tr>
<tr>
<td>Bandwidth Vis Area</td>
<td>(2, 14)</td>
<td>3.051</td>
<td>0.0795</td>
</tr>
<tr>
<td>Day</td>
<td>(1, 7)</td>
<td>1.058</td>
<td>0.3378</td>
</tr>
<tr>
<td>Attn Cond</td>
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<td>0.009</td>
<td>0.9263</td>
</tr>
<tr>
<td>Vis × Day</td>
<td>(2, 14)</td>
<td>0.17</td>
<td>0.8456</td>
</tr>
<tr>
<td>Vis × Attn</td>
<td>(2, 14)</td>
<td>1.044</td>
<td>0.378</td>
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<tr>
<td>Day × Attn</td>
<td>(1, 7)</td>
<td>3.988</td>
<td>0.086</td>
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<tr>
<td>Vis × Day × Attn</td>
<td>(2, 14)</td>
<td>1.816</td>
<td>0.199</td>
</tr>
<tr>
<td>Mean Vis Area</td>
<td>(2, 14)</td>
<td>0.348</td>
<td>0.7121</td>
</tr>
<tr>
<td>Day</td>
<td>(1, 7)</td>
<td>0</td>
<td>0.9856</td>
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<tr>
<td>Attn Cond</td>
<td>(1, 7)</td>
<td>0.742</td>
<td>0.4175</td>
</tr>
<tr>
<td>Vis × Day</td>
<td>(2, 14)</td>
<td>0.338</td>
<td>0.7191</td>
</tr>
<tr>
<td>Vis × Attn</td>
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<td>1.554</td>
<td>0.2458</td>
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<tr>
<td>Day × Attn</td>
<td>(1, 7)</td>
<td>0.962</td>
<td>0.3593</td>
</tr>
<tr>
<td>Vis × Day × Attn</td>
<td>(2, 14)</td>
<td>1.591</td>
<td>0.2384</td>
</tr>
</tbody>
</table>

Significant effects shown in italics.
of enhanced responses in orientation channels tuned around the relevant stimulus feature and to attenuated responses in orientation channels tuned progressively farther away from the relevant stimulus (compare Fig. 5, A to B). Thus measuring the entire tuning profile might provide improved sensitivity to detect learning-related changes in the amplitude of sensory responses. In addition, and perhaps more importantly, our display contained multiple competing stimuli (a central RSVP stream and a peripheral grating), and competition between multiple stimuli has been previously shown to amplify the magnitude of attentional modulations in visual cortex (e.g., Moran and Desimone 1985; Motter 1993; Desimone and Duncan 1995; Kastner et al. 1998; Awh et al. 2003; Reynolds and Desimone 2003; Serences et al. 2004; Gál et al. 2009). Thus the degree of interstimulus competition might be a key factor in determining the magnitude of sensory modulation during PL. In either case, we believe that the current evidence, both from our study and from others, firmly suggests that PL enhances sensory modulation as well as enhanced readout, and future studies will need to directly determine how much each mechanism contributes to behavioral indexes of PL, particularly as a function of the degree of competition between relevant and irrelevant stimuli in the visual field.

The present observation of a training-related increase in feature-selective attention effects is consistent with several previous studies that focused on PL for highly specific visual features (reviewed in Seitz and Dinse 2007; Roelfsema et al. 2010; Byers and Serences 2012). In particular, the present data are consistent with previous suggestions that top-down attentional modulations play a key role in both context-dependent effects on sensory processing, PL, and attenuating responses evoked by task-irrelevant features (Gilbert et al. 2000; Crist et al. 2001; Schoups et al. 2001; Li et al. 2004; Vidnyánszky and Sohn 2005; Gál et al. 2009; Mukai et al. 2011; Gilbert and Li 2012). For example, Gilbert and Li (2013) summarize evidence for top-down attentional control and recurrent feedback connections as a mechanism for changing early sensory responses based on task goals; a pattern that is present even in the pretraining orientation-selective response profiles described here. However, our data suggest a further key role of task context in gating posttraining sensory responses, as enhanced responses to trained stimuli were primarily elicited when the orientation stimulus is task relevant and not when the orientation stimulus is merely present (i.e., in the attend RSVP condition; Gilbert et al. 2000; Li et al. 2004; Gilbert and Li 2012). Furthermore, the nature of the neural changes associated with PL may be dependent on the context in which subjects were trained, suggesting that training with more irrelevant distractors could lead to even larger attentional modulations, both before and after learning (Luck et al. 1993; Motter 1993; Kastner and Ungerleider 2000; Li et al. 2004; Vidnyánszky and Sohn 2005; Gál et al. 2009; Gilbert and Li 2012).

Recently, Jehee et al. (2012) used fMRI to show that the ability of individual voxels in V1-V4 to discriminate between two similar orientations was improved when the oriented stimulus was attended compared with when it was unattended. However, this improvement was specific to both the trained orientation and stimulus location, so the implication of their results to situations in which training is focused on improving the discriminability of a larger class of stimuli is unclear. In contrast, we addressed this complementary question by exploiting the joint information encoded by large-scale populations to show that generalized orientation learning improves the amplitude of feature-based modulations in early visual cortex. Thus the current results demonstrate that PL modifies population-level orientation tuning profiles via enhanced attentional gain and that these population-level modulations provide computational constraints on models of PL in more complex scenarios.

In the present study, we observed a qualitative attenuation of responses to the grating stimulus when subjects were performing theattend-RSVP task (see blue line in Fig. 5B; although note that we cannot compare pre- and posttraining response amplitude levels quantitatively in the attend-RSVP condition due to learning-related changes in the nature of the sensory stimulus, see RESULTS). At first glance, this observation seems inconsistent with prior work showing PL even for task-irrele-

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**Fig. 7.** Parameter estimates from the best fitting von Mises function for each individual visual area (V1, V2, V3). Left: amplitude of best-fitting von Mises function for the attend-orientation (gray) and attend-RSVP (blue) tasks during the pretraining (left) and posttraining (right) scan sessions. Middle: bandwidth of the best-fitting von Mises function in the attend-orientation (gray) and attend-RSVP (blue) tasks during the pretraining (left) and posttraining (right) scan sessions. Right: baseline of the best-fitting von Mises function in the attend-orientation (gray) and attend-RSVP (blue) tasks during the pretraining (left) and posttraining (right) scan sessions. All error bars are ± 1SE.
vant stimuli when they are paired with the presentation of a concurrent relevant or rewarding stimulus (Seitz and Watanabe 2005; Seitz et al. 2009; Franko et al. 2010). However, task-irrelevant PL seems to occur only when the irrelevant stimulus does not strongly compete or interfere with the processing of the relevant attended stimulus (Watanabe et al. 2001; Seitz et al. 2006, 2009; Tsushima et al. 2008; Choi et al. 2009; Seitz and Watanabe 2009; Huang and Watanabe 2012; Leclercq and Seitz 2012a,b). This criterion is not likely met in our study, as the grating was highly salient and it surrounded the relatively low-salience central RSVP stream. Thus this stimulus configuration likely led to a high degree of interstimulus competition, and in turn this competition may have blocked task-irrelevant PL effects on the oriented grating when subjects were attending the central RSVP stream.

In previous reports (e.g., Regan and Beverley 1985; Seung and Sompolsinsky 1993; Schoups et al. 2001), including work from our own laboratory (Scolari and Serences 2009, 2010; Scolari et al. 2012), the performance of a fine discrimination task between similar orientations has been shown to mediate the gain of “off-channel” neural populations, or those neurons that are tuned just away from the to-be-discriminated feature. From an information-theoretic viewpoint, this is optimal because these off-channel neurons have a steeper tuning function around the discriminanda and should thus undergo a larger change in firing rate to the two stimulus alternatives (see Scolari and Serences 2009 for more discussion). Thus we might have expected such off-channel modulations in the present study to be enhanced with PL. However, in experiment 1 of Scolari et al. (2012), we demonstrated that off-channel gain, at least as assessed using fMRI and the same analysis approach and general paradigm used here, is not observed when the direction of the orientation offset is unknown in advance (i.e., the subject does not know whether to attend to and expect a clockwise or a counterclockwise rotation). In experiment 2 in the same article, we then demonstrated a robust off-channel gain effect when we precued subjects about the rotational offset of the oriented stimuli in advance. Given that the present task closely mimics experiment 1 from Scolari et al. (2012) in which no precue was given, we did not expect to see off-channel gain in early visual areas in the present study and indeed no robust evidence for such an effect was observed.

Although we observed an increase in the overall amplitude of orientation-selective responses in early visual areas (Fig. 5C), we did not observe any training-related changes in the mean BOLD response computed across all voxels in each ROI (Fig. 4). Several previous reports also failed to observe changes in the mean BOLD response with PL (Yotsumoto et al. 2008; Zhang et al. 2010a; Jehee et al. 2012). Note, however, that the presence of enhanced feature-based attention effects (Figs. 5 and 6) can still be observed even if there is no net change in the magnitude of the mean HRF that is computed based on the average across all voxels. For example, we observed enhanced responses in channels tuned to the relevant stimulus and attenuated responses in channels tuned away from the relevant stimulus (Figs. 5B and 6). Thus increases and decreases in the channel responses roughly cancel out and we would not predict a change in overall HRF amplitude. In addition, others have suggested that learning leads to improved coding for specific features even in the absence of a change in mean HRF amplitude, as PL might reduce response variability (which would effectively increase the signal-to-noise ratio of the HRF without changing its overall magnitude; Jehee et al. 2012). Finally, it is possible that the amplitude of the mean BOLD response is modulated by PL but that early learning-induced increases in BOLD amplitude return to baseline with further training (Yotsumoto et al. 2008). Thus we may not have observed changes in HRF amplitude because our posttraining fMRI session took place after the HRF returned to pretraining baseline levels.

In summary, we used a forward encoding model to make inferences about how PL influences the shape of population-level orientation tuning functions based on the multivariate response profiles in visual cortex (Serences and Saproo 2012). We show that PL leads to a selective increase in the amplitude of orientation-selective tuning profiles in V1-V3 with training. This amplitude increase corresponds to an increase in the dynamic-range (or entropy) of orientation-selective response profiles within these regions. In turn, increasing the dynamic range of feature-selective response profiles should, in theory, increase the information content of these population-response profiles and thus the separability of responses evoked by stimuli rendered at different orientations (i.e., an amplitude increase should magnify the difference between mean responses evoked by two nearby orientations; Saproo and Serences 2010, 2014).

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: A.B. and J.T.S. conception and design of research; A.B. performed experiments; A.B. analyzed data; A.B. and J.T.S. interpreted inferences about how PL influences the shape of population-level orientation tuning functions based on the multivariate response profiles in visual cortex (Serences and Saproo 2012). Thus we may not have observed changes in HRF amplitude because our posttraining fMRI session took place after the HRF returned to pretraining baseline levels.

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AUTHOR CONTRIBUTIONS

Author contributions: A.B. and J.T.S. conception and design of research; A.B. performed experiments; A.B. analyzed data; A.B. and J.T.S. interpreted results of experiments; A.B. prepared figures; A.B. drafted manuscript; A.B. and J.T.S. edited and revised manuscript; A.B. and J.T.S. approved final version of manuscript.

REFERENCES


