An integrated reweighting theory of perceptual learning

Barbara Anne Dosher⁎, Pamela Jeter⁎, Jiajuan Liu⁎, and Zhong-Lin Lu†

⁎Department of Cognitive Sciences and †Center for Cognitive Neurosciences, University of California, Irvine, CA 92617; and ‡Department of Psychology, The Ohio State University, Columbus, OH 43210

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Improvements in performance on visual tasks due to practice are often specific to a retinal position or stimulus feature. Many researchers suggest that specific perceptual learning alters selective retinotopic representations in early visual analysis. However, transfer is almost always practically advantageous, and it does occur. If perceptual learning alters location-specific representations, how does it transfer to new locations? An integrated reweighting theory explains transfer over retinal locations by incorporating higher level location-independent representations into a multi-level learning system. Location transfer is mediated through location-independent representations, whereas stimulus feature transfer is determined by stimulus similarity at both location-specific and location-independent levels. Transfer to new locations/positions differs fundamentally from transfer over stimulus features. Position transfer is mediated through reweighting of more broadly tuned location-independent representations, whereas transfer between different stimulus features reflects the similarity, conflict, or independence of the optimal weight structures in two tasks for both location-specific and location-independent representations. The perceptual learning mechanism is implemented as augmented Hebbian reweighting (13, 14) that dynamically optimizes connections between stable stimulus representations and a task decision. Reweighting operates on both levels of representations simultaneously. This is a computational model of perceptual learning that uses both multiple levels of representation and multiple locations to make predictions about location and feature transfer. The IRT predicts differential transfer to new features, locations, or both. Learned improvements in a task for the same feature transfer relatively well to a new location based on learned reweighting of the location-independent representations. Switches of feature in the same location show far less transfer as they require learning either new or conflicting weight structures for both location-independent and location-specific representations. Switches of both feature and location may show intermediate transfer if conflicting weight structures must be learned for the location-independent representations. Direct tests of the IRT predictions lead to our experiment. The computational IRT provides quantitative predictions for learning and transfer specialized for each experimental protocol. A computational model is necessary to generate predictions for learning and transfer that reflect the stimuli and judgment (15), the extent of initial training (16), and other aspects of each experimental protocol.

Almost all perceptual tasks exhibit perceptual learning, improving people’s ability to detect, discriminate, or identify visual stimuli. These improvements due to practice are the basis of visual expertise. Practice improves the ability to perceive orientation, spatial frequency, patterns and texture, motion direction, and other stimulus features (1–4). Learned perceptual improvements generally show some specificity to the feature and to the retinal location of training. Specificity of trained improvements to retinal location and feature in behavioral studies of texture orientation (5, 6) or simple pattern orientation judgments (7, 8) inspired early researchers to posit that practice altered the responses of early visual representations (V1/V2) with small receptive fields, retinotopic structure, and relatively narrow orientation and spatial frequency tuning (6).

However, the generalization of learned perceptual skills over retinal locations is almost always practically advantageous, and is sometimes observed (9). Whether perceptual learning reflects changes in retinotopic representations in early visual cortical areas (6) or alternatively—as we have suggested elsewhere—is primarily accomplished through selective readout or reweighting of stable early representations (10–14), the theoretical challenge is not explaining specificity, but rather explaining how and under what circumstances learning transfers over locations.

An integrated reweighting theory (IRT) of perceptual learning and transfer, developed and tested here, is designed to account for learning at multiple locations (Fig. 1) and other related learning phenomena. The IRT proposes an architecture of perceptual learning in which higher level location-independent representations are trained at the same time as location-specific representations. Transfer to new retinal positions/locations is fundamentally different from transfer over stimulus features. Position transfer is mediated through reweighting of more broadly tuned location-independent representations, whereas transfer between different stimulus features reflects the similarity, conflict, or independence of the optimal weight structures in two tasks for both location-specific and location-independent representations. The perceptual learning mechanism is implemented as augmented Hebbian reweighting (13, 14) that dynamically optimizes connections between stable stimulus representations and a task decision. Reweighting operates on both levels of representations simultaneously. This is a computational model of perceptual learning that uses both multiple levels of representation and multiple locations to make predictions about location and feature transfer. The IRT predicts differential transfer to new features, locations, or both. Learned improvements in a task for the same feature transfer relatively well to a new location based on learned reweighting of the location-independent representations. Switches of feature in the same location show far less transfer as they require learning either new or conflicting weight structures for both location-independent and location-specific representations. Switches of both feature and location may show intermediate transfer if conflicting weight structures must be learned for the location-independent representations. Direct tests of the IRT predictions lead to our experiment. The computational IRT provides quantitative predictions for learning and transfer specialized for each experimental protocol. A computational model is necessary to generate predictions for learning and transfer that reflect the stimuli and judgment (15), the extent of initial training (16), and other aspects of each experimental protocol.

Previous behavioral studies of transfer after perceptual learning have generally changed either stimulus feature, such as orientation, or position at the task switch, but not both (5, 7, 8, 10, 11, 15, 17, 18). Schoups et al. (7) were the first to claim surprising specificity of learned peripheral orientation discrimination to positions separated by only a few degrees of visual angle. However, a review of all of the literature suggests a more nuanced picture. Many cases (8, 10, 11) exhibit only partial specificity—and so partial transfer—to visual field quadrant, or from preliminary foveal training to peripheral locations, with some residual specificity.

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1To whom correspondence should be addressed. E-mail: bdosher@uci.edu.

2Present address: Department of Ophthalmology, Wilmer Eye Institute, Johns Hopkins University, Baltimore, MD 21202.

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to each location (7), even when both orientations and locations are switched (5, 15). No prior study provides ideal experimental comparisons; still the literature overall is suggestive of greater partial transfer of learning when both reference angle and location are switched (15). This leaves room to see either more or less transfer and specificity for the other conditions. Throughout practice, discrimination was tested with and without external noise in the stimulus (“no noise” and “high noise”; Fig. 2), to assay learned stimulus enhancement and external noise exclusion, respectively (10, 11, 18, 19). Performance with and without external noise reveals different limiting factors in learning that can show distinct profiles of learning and transfer (18, 19, 23). Accounting simultaneously for both high and low noise within the context of the detailed training protocol of the experiment is a strong challenge for quantitative tests of the IRT model.

Fig. 2 shows average contrast thresholds to achieve 75% correct as a function of practice for the initial training phase (Fig. 2, Left) and the postswitch transfer phase (Fig. 2, Right). The ± error bars were estimated from the data using Monte Carlo methods (n = 1,000). Power function improvements in contrast thresholds, fit by least-squares methods, are shown as smooth curves. Gabor patches are harder to see in the presence of visual noise and have higher threshold contrasts in both the initial training phase [(P(1, 64) = 149.24, P < 0.0001) and the postswitch transfer phase [F(1, 64) = 79.57, P < 0.0001]. (The IRT model fits low and high external noise conditions jointly with the same model parameters; see below.) Observers were randomly assigned to groups, so the initial performance of the groups should be statistically equivalent, and it is [F(2, 30) = 0.393, P > 0.6 in high noise and F(2, 30) = 0.454, P > 0.6 in no noise]. Initial training data in each noise condition and all groups were well fit by the same power function learning curves [F(6, 15) = 0.1].

Results

Observers judged small differences in the orientation of Gabor patches in periphery as clockwise or counterclockwise relative to an oblique reference angle (R° ± 5°) (see Fig. S1 for stimuli). Observers were assigned randomly to three groups. After eight blocks (two per session) of practice with one set of orientations and positions, observers were switched in one of three ways (P, O, or OP), and trained for another eight blocks. All together, each observer completed about 10,000 trials (Materials and Methods). High-precision orientation judgments, such as (R° ± 5°), yield partial specificity and partial transfer of learning when both reference angle and location are switched (15). This leaves room to see either more or less transfer and specificity for the other conditions. Throughout practice, discrimination was tested with and without external noise in the stimulus (“no noise” and “high noise”; Fig. 2), to assay learned stimulus enhancement and external noise exclusion, respectively (10, 11, 18, 19). Performance with and without external noise reveals different limiting factors in learning that can show distinct profiles of learning and transfer (18, 19, 23). Accounting simultaneously for both high and low noise within the context of the detailed training protocol of the experiment is a strong challenge for quantitative tests of the IRT model.

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2.09, \( P = 0.12, F(6, 15) = 0.733, P = 0.63 \), in no noise and high noise, respectively.

Orientation discrimination contrast thresholds improved with practice in the initial training phase in both high external noise and no external noise tests (all \( P < 0.001 \), by \( t \) test). Performance also improved with practice in the transfer phase in both high noise (all \( P < 0.001 \)) and no noise (\( P < 0.001, 0.003, \) and 0.05, respectively). If practice only changes the tuning of early visual representations, then stimuli should be represented with independent neural coding in all groups, and all conditions should show high, nearly maximal, levels of specificity. In contrast, in the IRT architecture, the three types of transfer will not in general be equivalent. Consistent with the IRT, the three transfer groups (O, P, and OP) differed in their transfer/specificity at the task switch. The same orientation stimuli switched to a new position (P, blue curves) led to the best performance at the switch point, showing considerable transfer or low specificity, consistent with transfer in the IRT through learned reweighting of location-independent representations that are still useful in the new location. Different orientation stimuli at the same position (O, red) led to the worst performance at the switch point, showing little transfer or high specificity, consistent with the need to learn either completely new or incompatible weights for the new orientations. The conditions differ at the first point after the task switch (100% transfer in both high and low noise (\( P \sim 0.013 \) and 0.09, respectively), and over all eight transfer blocks in high noise (\( P \sim 0.01 \)). The contrast thresholds for the position and orientation switch group (OP) were intermediate, and closely replicate the representations in the new location are independent of prior learning. Individual observer results were generally consistent with these patterns.

The practice effects on contrast thresholds were fit with power functions that estimate differential transfer; this quantitative analysis of the whole pattern of learning, detailed next, supports the conclusions above. Elaborated power functions, \( c(t) = \lambda \sim (t + tX)^{\alpha} + \rho \), provide an excellent account of threshold improvement for aggregate data (15, 16, 19), where \( c(t) \) is the contrast threshold at practice block \( t \), \( \alpha \) is the asymptotic (minimum) threshold after extensive practice, \( \lambda \) is the initial incremental threshold above \( \alpha \), \( \rho \) is the learning rate, and transfer of prior experience is summarized by transfer factor \( tX \), which is set to 0 for initial training (see ref. 15 for a description). The \( tX \)s quantify transfer in blocks, ranging in this experiment between zero (no benefit of prior training or full specificity) and eight (full transfer or no specificity). The estimates of \( tX \) at the task switch in high noise were \( \hat{tX} = 0.04, \hat{tX} = 0.59, \) and \( \hat{tX} = 2.47 \) (with \( \lambda = 0.56, \rho = 0.45, \alpha = 0.20, \rho = 0.865 \) and in low noise were \( \hat{tX} = 2.63, \hat{tX} = 0.37, \) and \( \hat{tX} = 1.09 \) (with \( \lambda = 0.58, \rho = 1.06, \alpha = 0.08, \rho = 0.945 \)). The three groups share \( \lambda \), \( \alpha \), and \( \rho \). The initial performance, asymptotic level, and effective learning rates for each external noise level.

Transfer is very high (transferring about six of eight blocks) for position switches (P), low (about one of eight blocks) for orientation switches (O), and intermediate (about 2.5 of 8 blocks) for changing both (OP) in high external noise, and about half these values in low noise trials. Correspondingly, performance level at the switch estimated from independent power functions were \( \hat{tX} = 0.30, \hat{tX} = 0.48, \) and \( \hat{tX} = 0.36 \) in high noise (with baseline \( \hat{tX} = 0.55 \) in the initial learning phase, \( r^2 = 0.915 \)) and were \( \hat{tX} = 0.12, \hat{tX} = 0.27, \) and \( \hat{tX} = 0.18 \) in low noise (with baseline \( \hat{tX} = 0.38, r^2 = 0.959 \)) (all \( P < 0.0001 \) by nested model tests). In sum, the power function analyses are consistent with the prior analyses and provide quantitative estimates of transfer.

Next, we develop a computational implementation of the IRT theory of perceptual learning and transfer. Our previous models of perceptual learning explain perceptual learning in a single location as incrementally optimized reweighting of outputs of early visual representations to influence a perceptual decision (10, 11, 24). The representations themselves often remain unchanged (6). A review of the literature in neurophysiology is broadly consistent with this idea (12), although modest representation retuning may also sometimes occur. A representation system (13, 14) operates on images of the experimental stimuli and computes activations of orientation and spatial-frequency tuned representation units. A decision unit integrates the weighted activation of these units and (nonlinearly) selects a behavioral response (i.e., “left” or “right” orientations). Connection weights are incrementally updated on each trial of a simulated version of the actual experiment through a Hebbian mechanism, augmented by feedback and bias correction. This augmented Hebbian reweighting model (AHRM) accounts for perceptual learning in alternating noise backgrounds (13), for the role of feedback (14, 25, 26) (see ref. 12 for a review), for the effects of external noise (11, 18), and for differential magnitudes of learning in high and low noise tests (11, 18). This original AHRM gives a powerful account of perceptual learning under varying training conditions for a single location. It provides no account for transfer of perceptual learning to new locations.

The IRT and architecture were developed to model learning and transfer across as well as within locations. This architecture has a broadly tuned location-independent representation as well as location-specific representations. The IRT simulation uses augmented Hebbian learning (13, 14) to simultaneously optimize the weights on location-independent representations and location-specific representations. The representation system for oriented pattern stimuli (such as the Gabors in the experiment) computes the normalized activation of noisy spatial frequency and orientation-sensitive units (see SI Materials and Methods, Model Implementation of the Integrated Reweighting Theory). Learning transfers to a new location or position when performance in a new location inherits useful location-independent weights; subsequent improvement occurs because the location-specific weights in the new location need to be learned. To summarize again, switching orientation in the same location changes weights for the new orientation but not for the old, whereas switching weights for the new orientation (training) and transfer (or interference) depends on the consistency, independence, or inconsistency of the optimal weight structures for the two sets of stimuli (14, 27). An IRT account of transfer of spatial, vernier, or bisection judgments (28, 29), or motion direction, would require alternative representation system modules suited to those tasks, but the architectural principle of the theory is general. Similarly, the details of the learning algorithm could be altered while retaining the general principles of the proposed architecture and theory.

The IRT simulation incorporates representation modules from the earlier single-location model (13). It takes an image and computes activations in different spatial-frequency and orientation tuned units that span the stimulus space via coarse sampling. Bandwidths are set from physiological estimates of early cortical areas, and we incorporate nonlinearities, internal noises, and selection of the spatial region of the oriented Gabor stimulus. The location-independent representations are noisier and more broadly tuned. The tradeoff for representing information from many locations is a reduction in the precision. Broader tuning is also motivated by the role of precision in the specificity of transfer to new locations, as well as by physiology (15). The weighted activations and input from a bias-control unit are passed through a nonlinear activation function to generate a binary response (i.e., left or right) on each trial. Weights from both the location-specific and location-independent units to the decision unit are updated after each trial. Feedback improves
learning in low accuracy conditions, but is not necessary for learning if the internal response without it is often correct. The model and related equations are described in SI Materials and Methods.

Examples of activation computed for the location-specific and the more broadly tuned location-invariant IRT representations are shown in Fig. S2. Best fitting simulated predictions of the IRT, shown in Fig. 3, provide a close account of the average human data ($r^2 = 0.952$), with model parameters listed in Table 1.

The low noise (Fig. 3, Left) and high noise (Fig. 3, Right) test data are separated for clarity of the graph, but they are intermixed in both the experiment and the modeling. Many of the general representation parameters were set a priori; others such as the learning rate are used to fit the observed rate of perceptual learning. The IRT model correctly predicts the ordinal patterns of the different transfer conditions under essentially all tested parameter sets; the fine-tuning of parameters matched performance levels and learning rate more closely. Internal representation noise parameters differed very slightly between the three subject groups to account for sampling differences; all other parameters are constant. Simulated model runs use random trial histories and response choices from the specific experimental design; incorporating observer variability in parameters would broaden the confidence bands, but not alter the basic pattern of predictions.

Perceptual learning pruned weights on irrelevant orientations and amplified weights for informative orientations of both location-specific and location-independent units—as seen in the initial weights, weights at the switch, and weights at the end of training on the new task (Fig. S3, SI Materials and Methods). Performance transfers over position via the learned location-independent weights, then all weights, including those for the new location-specific representations, are further optimized. For switches of orientation, both the location-specific and the location-independent weights are tuned for now irrelevant orientations, and both require learning of the new orientations, and unlearning of those previously learned weights that are inappropriate for the new orientations. If both dimensions are switched, then the location-specific weights are learned anew, whereas the location-independent weights must be retrained. This eliminates any conflict in learned weights between the training and the transfer tasks for the location-specific representations.

Discussion
Specificity to trained stimuli and locations is central in claims about neural mechanisms of perceptual learning. Specificity and transfer are also important in determining the value of perceptual learning for training of expertise and rehabilitation. Qualitative theories claiming that perceptual learning adapts or retunes neurons in early visual cortex imply widespread observations of specificity to position and stimulus features and equal and high specificity for all task switches involving distinct neural populations. A consideration of the literature led us instead to hypothesize that transfer to new locations was mediated by reweighting of information from location-independent representations, and to develop and test a new IRT and transfer architecture. We specified broader tuning and higher noise for the location-independent representation based on findings in the literature that the required precision of the transfer task is an important determinant of transfer over locations; high-precision tasks benefit less from transfer (5, 15).

The experiment directly compares switches of position only (P), orientation only (O), and both dimensions (OP) within the same task and training structure. Our findings of greater specificity for orientation changes than for position changes are generally in line with the prior literature (7, 8, 18) (but see ref. 17), while controlling for extraneous factors in prior comparisons. The results are qualitatively and quantitatively consistent predictions of the IRT. No noise and high noise testing were intermixed in this study and therefore influence and reflect the same learned weight structures. High noise conditions naturally produced the larger magnitude of perceptual learning and differences in specificity observed under noisy test conditions.

### Table 1. Parameters of the best-fitting IRT model

<table>
<thead>
<tr>
<th>Parameters set a priori</th>
<th>Parameter values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orientation spacing $\Delta \theta$</td>
<td>15°</td>
</tr>
<tr>
<td>Spatial frequency spacing $\Delta f$</td>
<td>0.5 octave</td>
</tr>
<tr>
<td>Maximum activation level $A_{max}$</td>
<td>$\pm 1$</td>
</tr>
<tr>
<td>Weight bounds $w_{min}$, $w_{max}$</td>
<td>$\sigma = 2.5e^{-7}$, $3.5e^{-6}$</td>
</tr>
<tr>
<td>Location-specific initial weights scaling factor $w_{init}$</td>
<td>0.127</td>
</tr>
<tr>
<td>Location-independent initial weights scaling factor $w_{initI}$</td>
<td>0.02</td>
</tr>
<tr>
<td>Activation function gain $\gamma$</td>
<td>3.5</td>
</tr>
<tr>
<td>Location-specific orientation bandwidth $h_{\theta}$</td>
<td>30°</td>
</tr>
<tr>
<td>Location-independent orientation bandwidth $h_{\thetaI}$</td>
<td>48°</td>
</tr>
<tr>
<td>Location-specific frequency bandwidth $h_{f}$</td>
<td>1 octave</td>
</tr>
<tr>
<td>Location-independent frequency bandwidth $h_{fI}$</td>
<td>1.6 octave</td>
</tr>
<tr>
<td>Radial kernel width $h_{r}$</td>
<td>2 dva</td>
</tr>
</tbody>
</table>

Parameters adjusted for the data

- Normalization constant $k$ | 3e-6 |
- Scaling factor $a$ | 1 |
- Location-specific internal noise 1 $\sigma_1$ | 2.5e-7 |
- Location-specific internal noise 2, $\sigma_2$ | 6e-4 |
- Location-independent internal noise 1 $\sigma_{1I}$ | 3.5e-6 |
- Location-independent internal noise 2 $\sigma_{2I}$ | 0.15 |
- Decision noise $\sigma_d$ | 0.01 |
- Learning rate $\eta$ | 6e-4 |

Location specific internal noises are for the three transfer conditions: P, O, and OP. dva, degrees of visual angle.

![Fig. 3. Predictions of the best-fitting IRT with the experimental data points. Model parameters of the best-fitting model were estimated by grid search methods and are listed in Table 1.](image-url)
reflecting the impact of external noise on imperfectly tuned weight templates for the tasks. If trained separately (18, 23), noisy test environments limit the ability to find a stable optimized weight structure (10, 11). Transfer of stimuli or tasks within the same location are accounted for within the same IRT architecture. That consistency of weight structures determined stimulus/task transfer was an explicit prediction of the AHMR for perceptual learning in training locations, necessary to account for persistent switch costs in alternating noise conditions (13, 14) (see also refs. 12, 27). Parallel predictions would hold for tasks other than orientation judgments, such as spatial, vernier, pattern, motion, or texture judgments, although several of these require a different representation subsystem.

The computational implementation of the IRT architecture makes it possible to generate predictions for and understand apparently inconsistent results based on the exact details of the experimental paradigm. The exact extent of training and transfer can depend on the amount of training, the accuracy of performance during training, the availability of feedback, and the mixture and specific schedules of training different stimuli and tasks. For example, our results are potentially related to, but differ from those of ref. 21, which reports nearly full transfer of an orientation task to a new transfer location after “pretraining” that primes the second location, suggesting to those authors a role for intermediate-level coding in visual perceptual learning.

The IRT architecture is extensible—it should make predictions about this and many other transfer phenomena, such as the “double training” method. Several such cases are being investigated in their own computational studies (30), where the IRT framework has accounted for several of the so-called double-training results as learned task-specific reweighting followed by up-regulation of location-independent weights through training with tasks requiring broad tuning. Details of the IRT implementation may need to evolve as this literature is expanded.

Neurophysiologists have also sought the neural signature of perceptual learning of orientation (31–35). Single-unit responses in early visual cortex before and after perceptual learning report largely identical location, size, and orientation selectivity between trained versus untrained regions of V1 and V2 (but see refs. 25, 36). Among these, a small change in slope in V1 neurons (34), not seen in other cases, is often cited as key evidence for chiasmatic or other pre-reaching changes in neurons primarily responsive to the trained orientation. Any small alterations in early visual representations following extensive training do not account for the large behavioral changes (15). In contrast, alterations in tuning curves have been seen in V4 (35). Analogously, in a visual motion task, extensive training left sensory responses in MT largely unaffected, but altered those of lateral interparietal cortex (LIP) (37). Overall, the neurophysiology suggests that although small changes in very low-level representations may sometimes occur, they are insufficient in general to account for the substantial behavioral changes. Instead, changes or decision structures at a higher level of the visual hierarchy are suggested (12); or perceptual learning may alter feed forward connections and correlation structures, possibly before V1 (38). The neurophysiology has examined changes in cortical regions as the result of training for a single task in a single location, and has not widely studied transfer and subsequent retraining.

The IRT and architecture provide an explanatory structure for and good quantitative fit to differential transfer for location and stimulus features. Transfer to new locations uses location-independent representations as the scaffold. We speculate that these location-independent representations are consistent with “object” representations of anterior inferotemporal (IT) in the ventral visual pathway. Our 5°-eccentric test locations are (center to center) separated by about 7°. In comparison, receptive field sizes at similar eccentricities are estimated at less than 1° for V1, 1–2° for V2, and 3–4° for V4 (39), although some estimates are as high as 6° for V4, so position transfer in this experiment seems more consistent with properties of IT (40–42). This parallels conclusions that learning in the motion system localizes to LIP rather than middle temporal area (MT) (37). Visual psychophysics generates critical information about functional properties of perceptual learning and transfer that support conjectures about neural substrate that need to be tested and refined with physiological or brain imaging investigations.

The IRT framework does not aim to reconstruct detailed neural pathways of the visual system or the decision-making and action-selection circuits that collectively produce the behavior. It is inspired by computational models of V1, V4, and higher visual areas, whereas tuning properties of the representational units reflect tuning properties in these cortical regions (43, 44). Our design strategy is to simplify the model to essentials and test the ability to predict the patterns in data. Further model development might take several directions. Although some perceptual learning paradigms such as the current study did not require consideration of recurrent connections (38), recurrent connections from decision to sensory representation units may play a role in segmentation, attention, and conscious awareness (45, 46), and future studies may incorporate them to account for the properties of learning in other paradigms as another form of learning through reweighting. Applications of the IRT in different stimulus domains, such as motion direction discrimination or vernier, would require representation modules appropriate for those domains. Also, more complex experimental designs are likely to require attention gating of different inputs to the decision. Finally, the current IRT architecture approximated location-independent activation by submitting the stimulus directly to the location-independent units. The development of a full hierarchical stimulus analysis in which the location-independent units receive their input from location-dependent units would itself be a major research project. However, the current IRT architecture provides a strong computational framework that can make predictions about a wide range of transfer phenomena.

Conclusions

Dosher and Lu, and others (10–14, 24) suggested an alternative to altered early cortical representations in visual perceptual learning—the “rewriting hypothesis”—in which perceptual learning incrementally optimizes the connections between sensory representations and decision. Most quantitative models of perceptual learning are based on reweighting or some other form of selection from stable early representations (13, 14, 26, 29, 47–50). As learning continues, only the most relevant neural representations survive in decision. Even if early representations are slightly modified, reweighting will be necessary to optimize performance—indeed reweighting will be all of the more necessary if sensory representations are altered. The IRT models transfer through an expanded architecture incorporating both location-specific and location-independent representations for both original learning in a single retinal position and transfer to new positions and stimulus features. The architecture implies a special status for transfer over locations based on the location-independent representations of midlevel visual analysis, validated in the current experiment. It provides a theoretically motivated basis for considering the quantitative and qualitative properties of transfer in a wide variety of task combinations. The computational IRT model makes quantitative predictions for learning and transfer that are sensitive to the exact stimuli and the details of the training procedure, providing a framework for understanding new training paradigms. Application of the model to each new experimental condition will further test the range of phenomena explained by this perceptual learning system.
Materials and Methods

Observers discriminated the orientation (±5° clockwise or counterclockwise from −35° or +35°) or Gabor patches presented either with or without external noise either in the NWSE or NESW corners (5.67° eccentric) on a computer screen. Contrast thresholds at 75% correct were measured using adaptive staircase methods. After training for four sessions (4,994 trials) on one task, they switched orientation, position, or both (O, P, or OP with 12, 11, and 10 observers) and trained for four sessions. Error feedback was provided. Details are in the SI Materials and Methods.

The IRT Matlab simulation takes grayscale images, computes activity in location-specific and location-independent representation units, generates a response, and then updates the weights. The simulated experiment exactly replayed the procedure in the human experiment. Representation parameters were set a priori for the location-specific representations (13, 14), at bandwidths of 30° for orientation and 1 octave in spatial frequency, spaced every one-half octave, respectively. Bandwidths of location-independent representations, estimated from preliminary fits, were 1.6 times the location-specific values, and the activation function parameter γ was set to 3.5. Observed threshold learning curves were fit with a scaling factor (α), two parameters for internal additive noise (η1) and for internal multiplicative noise (η2), one each for location-specific, and one for location-independent representations, a decision noise (σc), and a learning rate (υ). These parameters were adjusted to yield the best root-mean-squares fit of the model to the average data (SI Materials and Methods). The predicted performance curves were based on 1,000 iterations of the model experiment.
Supporting Information

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SI Materials and Methods

Methods. Observers. Observers had normal to corrected-to-normal vision and provided written consent under a University of California, Irvine institutional review board protocol. They participated in 9,984 experimental trials per observer. Observers were randomly assigned to experimental groups (P, O, or OP, with 12, 11, and 10 completed observers, respectively).

Design. Observers discriminated the orientations of a Gabor (windowed sinewaves) tilted ±5° top clockwise (“right”) or counterclockwise (“left”) from a reference angle $R$ of either –35° or +55°. Test locations were on one or another diagonal (NW/SE or NE/SW) at 5.67° eccentricity. Zero noise and high noise test conditions were intermixed within each testing block. Observers were randomly assigned to switch group, initial reference angle, and training positions. They trained for eight blocks over four sessions in an initial task, switched tasks, and trained for another eight blocks or four sessions. Contrast thresholds were measured using adaptive staircase methods (SI Materials and Methods, Staircases) tracking 75% correct.

Apparatus. A Macintosh G4 using the internal 10-bit video card followed by spatial phase pooling and +x±y±C×two new noise frames) appeared within a 64×64 noise image had 2×2 pixel noise elements with Gaussian-distributed contrasts with mean value 0 and SD 0.33, newly generated for each frame and trial. Signal and noise images were combined at alternation at the frame rate (SI Materials and Methods, Procedure). A single Gabor appeared on any trial, preceded by 150 ms by a brief arrow indicating the test location. Stimuli were generated using MATLAB with PsychToolbox extensions.

Sample images and power spectra for the right stimuli (four angles, with and without external noise) are shown in Fig. S1. The signal Gabors and the external noise images were integrated via spatial phase {0°, 90°, 180°, 270°}. Based on estimates of cellular tuning bandwidths. The location-speciﬁc representations are essentially independent of orientation and only modulated by fast Fourier transform. This is followed by a half-squaring filter to each unit $h_i$ = 1 octave, and the bandwidth of the orientation tuning was set at $h_o$ = 30° (half-amplitude full-bandwidth). The location-specific representations used these values, whereas the more broadly tuned location-invariant representations used spatial frequency and orientation bandwidths of 1.6x those of the location-specific units.

The input image $I(x, y)$ is convolved with the filter for each unit by fast Fourier transform. This is followed by a half-squaring operation that generates phase-sensitive activation maps analogous to “simple cells,” followed by spatial phase pooling and inhibitory normalization (SI): $E(x, y, \theta, f) = \sum_\phi S(x, y, \theta, f, \phi) + e_1$ and $C(x, y, \theta, f) = \frac{E(x, y, \theta, f)}{1 + x^2}$, respectively. The noise term $e_1$ is Gaussian-distributed internal noise source with mean 0 and SD $\sigma_1$. The normalization pool $N(f)$, consistent with physiological reports, is essentially independent of orientation and only modestly tuned for spatial frequency. The value $a$ is a scaling factor, and $k$ is the saturation constant that operates at near-zero contrasts. Spatial phase is pooled for the orientation judgment task, where phase is not relevant, but it could be retained for judgments that are contingent on phase. The spatial activation maps are 79.4% and 70.7% correct, respectively, by reducing contrast by 10% after either three or two consecutive correct responses, and increasing contrast 10% after each incorrect response. Staircases were interleaved, one for each external noise level, target accuracy, and testing location. There were 1,248 trials per session, 672 in 3/1 staircases and 576 in 2/1 staircases organized into four blocks (84 and 72 trials per block for staircase for 3/1 and 2/1 staircases, respectively). Threshold contrast levels averaged an even number of reversals for each staircase sequence, excluding the first four or five, to limit bias. Averaging the 3/1 and 2/1 staircases tracks an overall performance level of ~75% correct. These were averaged over two blocks, to yield two larger block thresholds per session.

Model Implementation of the Integrated Reweighting Theory. The integrated reweighting theory (IRT) is a multichannel, multilevel network model to account for transfer of perceptual learning over location. Learning occurs through channel reweighting (2). The IRT architecture includes location-independent as well as location-specific representations. It incorporates computational modules from the prior augmented Hebbian reweighting model (AHRM) that modeled perceptual learning in a single location (3). The IRT makes predictions about transfer of perceptual learning, and also has implications (not tested in this study) concerning training task mixtures. Here we provide a description and equations for the representation subsystem and the learning system, following refs. 3, 4.

The representation subsystem consists of orientation- and frequency-selective units. The activation value $A(\theta, f)$ of the representation units corresponds to the normalized spectral energy in each channel. A set of retinotopic phase-sensitive maps $S(x, y, \theta, f, \phi)$ is computed for the input image $I(x, y)$:

$$S(x, y, \theta, f, \phi) = [R_{\theta, \phi}(x, y) \otimes I(x, y)]^2,$$

for units tuned to different spatial frequencies $f$, orientations $\theta$, and spatial phases $\phi$. We assumed five spatial frequency bands at $\{1, 1.4, 2, 2.8, 4 \text{ c/d}\}$, orientations sampled every 15°, or $\{0^\circ, \pm 15^\circ, \pm 30^\circ, \pm 45^\circ, \pm 60^\circ, \pm 75^\circ, 90^\circ(-=90^\circ)\}$, and four spatial phases $\{0^\circ, 90^\circ, 180^\circ, 270^\circ\}$. Based on estimates of cellular tuning bandwidths in primary visual cortex, the bandwidth of the spatial frequency tuning was set at $h_i = 1$ octave, and the bandwidth of the orientation tuning was set at $h_o = 30^\circ$ (half-amplitude full-bandwidth). The location-specific representations used these values, whereas the more broadly tuned location-invariant representations used spatial frequency and orientation bandwidths of 1.6x those of the location-specific units.
combined and weighted through a Gaussian kernel of radius $W_r$ commensurate with the size of the target Gabor. A second Gaussian-distributed noise of mean 0 and SD $\sigma_2$ reflects a second source of stochastic variability: $A'(\theta, f) = \sum_{x,y} W_r(x,y) \cdot C(x, y, \theta, f) + e_2$. These responses are then passed through an activation function with gain parameter $\gamma$ to limit the range of the activation of the representation units: $A(\theta, f) = \begin{cases} \frac{1}{1+e^{-\gamma x}} A_{\text{max}}, & \text{if } A' \geq 0 \\ 0, & \text{otherwise} \end{cases}$.

The system makes a behavioral decision on each trial by combining the sensory information in the activation pattern over the representation units in a single decision unit. The decision variable weights these inputs by the current weights $w_i$, including a top-down bias factor $b$ with weight $w_b$ : $u = \sum_i w_i A(\theta_i, f) - w_b b + e_d$, and includes random decision noise $e_d$ (Gaussian with mean 0 and SD $\sigma_d$). The “early” activation of the decision unit $o'$ is a sigmoidal function of the weighted activations $u$ with gain $\gamma'$ ($o = G(u) = \frac{1}{1+e^{-\gamma' u}} A_{\text{max}}$). A negative $o'$ maps to one response (left), whereas a positive $o'$ maps to the other response (right).

The weight structure is learned through updating on every trial. When feedback is available, the feedback $F$ is used to compute a new, late level $o$: $o = G(u + w_F F)$ (late). Learning occurs during this late phase (6). The effect of feedback depends upon its weight $w_F$. The late activation will go to its maximum ($\pm A_{\text{max}} = \pm 1$) with feedback ($F = \pm 1$), and the feedback weight is relatively high, whereas low feedback weight will only slightly shift activation in the direction of the correct response. If no feedback signal is present ($F = 0$), learning operates on the early decision activation ($o = o'$), which is usually in the intermediate range. For all but the lowest accuracy conditions, the weights still move statistically toward a more optimum weight distribution because the activations at decision are correlated with the correct response.

Learning occurs by updating the synaptic connection strengths $w_i$ from sensory representation units $i$ to the decision unit. The change in each weight, $w_i$, depends on the learning rate, $\eta$, the activation at the presynaptic connection, $A(\theta_i, f)$, the postsynaptic activation compared with its long-term average, $(o - \bar{o})$, and the distance of the weight from the minimum or maximum saturation value, $w_{\text{min}}$ or $w_{\text{max}}$. So the change in weight is: $\Delta w_i = (w_i - w_{\text{min}})[\delta_i] + (w_{\text{max}} - w_i)[\bar{o} - \bar{o} - \bar{o}]$, where $\delta_i = \eta A(\theta_i, f)(o - \bar{o})$, and the average of postsynaptic activation is $\bar{o}(t + 1) = \rho \bar{o}(t) + (1 - \rho) \bar{r}(t)$. The Hebbian term $\delta_i$ tracks systematic stimulus–response correlations rather than mere response bias. The Hebbian learning process is augmented not just by feedback (when it occurs), but also by a criterion control that tracks deviations of the recent response frequencies from 50% or the instructed presentation probabilities in the experiment. Top-down input from a bias unit $b$ feeds into the decision unit with weight $w_b$. The bias $b(t + 1)$ on each successive trial is a running average of responses $r(t)$, weighted exponentially with a time constant of 50 trials ($p = 0.02$), $r(t + 1) = \rho r(t) + (1 - \rho) b(t)$. Prior studies found more pervasive response biases, and correspondingly lower weights on adaptive criterion control, in the absence of feedback (4). Both bias control and feedback augment pure Hebbian reweighting. Bias control tracks the model’s responses, whereas feedback tracks external teaching signals. Bias control is more important to learning in the absence of trial-by-trial external feedback (4).

**Simulation Methods**

The IRT simulation, implemented in MatLab, takes grayscale images, computes activity in location-specific and location-independent representation units, generates a response, and then updates the weights. The simulated experiment exactly replayed the procedure in the human experiment. Filter spacing and orientation and spatial frequency bandwidth parameters, the radius of spatial summation, and several other parameters were set a priori for the location-specific representations (3, 4). The bandwidths of location-specific representations were $30^\circ$ for orientation and 1 octave in spatial frequency (full bandwidth at half height), every $15^\circ$ in orientation and every one-half octave in spatial frequency. The spatial frequency and orientation bandwidths of location-independent representations were set at 1.6 times the location-specific values based on preliminary fits to the data.

Typical activation patterns in location-specific and location-independent representations for the four oriented Gabor stimuli with and without external noise are shown in Fig. S2, with the patterns for the to-be-discriminated angles shown in the same panels for ease of comparison. The patterns vary for each sample of external noise and for different Gabor contrasts.

The performance levels and the learning curves from experimental data were fit with a scaling factor ($\alpha$), two parameters for internal additive noise ($\sigma_1$) and for internal multiplicative noise ($\sigma_2$), one each for location-specific and one for location-independent representations, a decision noise ($\sigma_3$), and learning rates ($\eta$). The model was optimized for the experimental data through successive grid search of the parameter values, as described below. Scaling parameters, noise parameters, and learning rate were adjusted to yield the best least-squares fit of the model to the average data. The parameter for the activation function of the decision unit, $\gamma$, was set to 3.5 after some initial testing. The predicted performance curves were based on 1,000 iterations of the model experiment.

The implementation of the IRT (SI Materials and Methods, Model Implementation of the Integrated Reweighting Theory) was fit to the data by grid search. To speed the simulation, large caches of the representation activations for stimulus images with different samples of external noise were computed for many Gabor contrasts. This image processing stage is very time-consuming, requiring up to several days of computation. Using precomputed caches in simulated learning runs avoided duplicating these time-consuming steps. Location-independent activations were computed by passing the images through the representation sub-system with broader bandwidths. The grid search of model parameters was also computationally intensive.

**SI Results**

Learning over practice is shown in the weight structures for the location-specific and location-independent representations. Fig. S3 displays the changes in weights from the beginning of the experiment (Fig. S3, Left) to the end of the first phase of training (Fig. S3, Center), and the end of the second phase of training (Fig. S3, Right). Learning shows increased weights for relevant spatial frequency and orientation channels and decreased weights for irrelevant channels for both the relevant location-specific units and the location-independent units. It also shows reduced reliance on location-independent representations. Subsequent training on the new task further trains the location-independent weights, and retrains the same location-dependent weights for orientation changes, or newly trains the second location weights for changes of just position, or position and orientation.

Examination of the model predictions over the many parameter combinations tested during optimization of the fit of the IRT model to the data essentially all showed the same ordinal pattern at transfer for the P, O, and OP conditions. So the ordinal predictions for the three switch conditions are quite general. Finding optimal parameters largely served to match overall level of performance and speed of learning. The weight structures showed similar qualitative patterns with learning.

Search grids were programmed that examined factorial combinations of the manipulated parameters, and looked for regions of higher values of fit. Finer grids within these regions were tested. Although we searched in most major regions of parameter combinations through these means, no search grid of this type can be exhaustive, so it is possible that some additional adjustment of
parameters would have further optimized the fit of the model to the data. For example, increasing noise terms generally increases thresholds, but differentially increasing additive noise increases thresholds in low noise more than that in high noise, whereas increasing multiplicative noise affects thresholds in high noise more. Increasing the scaling factor normally improves performance; however, if the scaling factor is too big, the saturation of activation makes the initial performance worse. Finally, if learning rate is increased, learning is faster. The profile of initial weights can also be manipulated. Such manipulation mainly changes initial performance of a training or transfer session. We finally chose one with moderate tuning to orientation and no tuning to spatial frequency, because it provided a better fit to the data. With a square-wave profile of initial weights—that is, less orientation tuning—the discrepancy of performance between zero and high noise is larger in the simulation than in the behavioral data. Specifically, a broad-tuned profile of initial weights worsens performance in high noise more by channeling more external noise into the decision unit. The amplitude of initial weights can also affect the initial performance.


Fig. S1. Sample images and power spectra from the experiment. A, B, C, and D show images corresponding with intermediate contrast Gabors without external noise tilted top left and right of the relevant implicit reference angle, with E, F, G, and H corresponding power spectra. I, J, K, and L show sample high noise tests with high contrast Gabors, with corresponding power spectra in M, N, O, and P. Power spectra show orientation on the angular axis (left tilting to right tilting) and spatial frequency (low to high) on the radial axis in polar coordinates.
Fig. S2. Average activation profiles in the location-specific and location-independent representations for the four oriented Gabor stimuli with and without external noise, with the two orientations to be discriminated shown in the same panels, with center orientation of filters on the x-axis, center spatial frequency of filters indicated by line color, and arbitrary activation units on the y-axis. The activation profiles show the largest discriminative information in critical orientations in the spatial frequency band closest to the stimulus, and the two neighboring bands.

Fig. S3. The connection weights on location-specific and location-independent representations over the course of learning: (A) initial weights; (B–D) weights at the end of the initial training phase for switches of position P, orientation O, and both orientation and position OP; (E) weights after the transfer phase for switches of position P; (F) weights after the transfer phase for switches of orientation O; and (G) weights after the transfer phase for switches of both position and orientation OP. Activity in spatial frequency bands 2.0 cpd (red), 1.0 cpd (blue), 1.4 cpd (green), 2.8 cpd (cyan), and 4.0 cpd (magenta).