CHAPTER

78

Mechanisms of Perceptual Learning

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ABSTRACT

Perceptual learning—improvement in the performance of a perceptual task as a function of practice or training—is a widely observed phenomenon that may have important practical and theoretical consequences. Perceptual learning may reflect plasticity in different levels of perceptual analysis, including changes in early visual, auditory, or somatic cortices, as well as higher-order changes in the weighting of information in task performance. Perceptual learning, as distinct from cognitive learning or strategy selection, often exhibits significant specificity to the trained stimuli or tasks, and is assessed by transfer (or, conversely, generalization) tests. At a behavioral level, the effects of perceptual learning on an observer's performance are characterized by external noise tests within the framework of noisy ideal observer models. In visual perceptual tasks, behavioral analysis, combined with evidence from neuroscience, supports perceptual learning at several levels that has the function of improving two separable mechanisms: tuning of the task relevant perceptual template (external noise exclusion) and enhancing the stimulus (reducing absolute threshold). These two mechanisms of improvement are separable in certain circumstances, but often coexist, albeit with decoupled magnitude. Many improvements due to perceptual learning reflect retuning through reweighting of unchanged early sensory representations.

I. PERCEPTUAL LEARNING

Large improvements in performance on even the simplest perceptual tasks as a result of practice or training have been observed in adult humans in virtually every sensory modality. Improvement in performance as a result of practice can have a profound impact on the speed or accuracy of performance in perceptual tasks. Perceptual learning has been documented in a wide variety of tasks, but the mechanism(s) by which performance is improved have been more difficult to identify. Transfer of perceptual learning to modified forms of the same task or to different related tasks has been the primary tool for discovering what is learned and inferring the physiological basis of that learning (Fahle and Poggio, 2002; Fine and Jacobs, 2002). Recently, however, transfer methods have been augmented by the use of observer models and external noise tests that identify more precisely the consequences and mechanisms of perceptual learning (Dosher and Lu, 1998; Dosher and Lu, 1999). The focus in this review is on visual perceptual learning.

A. Perceptual Learning in Visual Tasks

Since Gibson's (1969) influential review, learning effects in adults have been reported for the detection or discrimination of visual gratings, stimulus orientation judgments, motion direction discrimination, texture discrimination, time to perceive random dot stereograms, stereoacuity, hyperacuity, and vernier tasks (see Ahissar and Hochstein, 1998; Dosher and Lu, 1999 for reviews). Improvements in performance are claimed to reflect perceptual learning, as opposed to cognitive learning, strategy selection, motor learning, or automatization of stimulus-response relations (Schneider and Shiffrin, 1997) whenever the performance is shown to be specific to either a retinal location or to a basic stimulus dimension such as orientation or spatial frequency (Karni and Sagi, 1991).

B. Specificity of Perceptual Learning

Specificity to a retinal location, or to a stimulus feature such as orientation does provide a strong argument for the perceptual nature of learning. However, it is more difficult to unambiguously identify the mechanism of perceptual learning. It is more difficult still to infer the functional locus of that learning (Dosher and Lu, 1998; Mollon and Danilova, 1996), although strong claims have been made about plasticity in early visual areas (Karni and Sagi, 1991). Perceptual learning has been evaluated for specificity (or conversely, transfer) to retinal position, eye of origin, orientation or spatial frequency, and retinal size. Specificity of learning to retinal position is often observed in texture discrimination, phase discrimination, orientation discrimination, and visual search (see Fahle and Poggio, 2002). Position specificity is generally evaluated by visual quadrant (Dosher and Lu, 1999; Karni and Sagi, 1991); finer location specificity of one degree or less has also been reported in several tasks. Similarly, orientation discrimination and motion direction discrimination are at least partially specific to orientation, although sometimes transfer occurs for mirror reversed orientations or homologous locations across the midline. Whether task specificity or generalization obtains in a task has recently been postulated to depend on task difficulty (Ahissar and Hochstein, 1997; Liu and Vaina, 1998).

Such location specificity is associated by some (Karni and Sagi, 1991) with early locus in the visual system, perhaps V1, with small receptive fields (but see Mollon and Danilova, 1996 for a critique). Orientation specificity is also often associated with early visual areas (V1, V2). Specificity to the trained eye has been seen in a very few cases, and this also specifies early visual cortex as the relevant region of perceptual coding. Specificity of perceptual learning to a retinal location or orientation does implicate representations early in the visual system, but the conclusion that such specificity implicates plasticity or perceptual retuning in those early visual areas is by no means obligatory (Dosher and Lu, 1998; Dosher and Lu, 1999; Mollon and Danilova, 1996). Instead, it may be the connections between the early visual system representations and decision processes at higher levels that embody system plasticity. This issue is relevant in the consideration of the physiological evidence.

C. Task Compatibility

Protocols for learning two or more interrelated perceptual tasks may also provide constraints on the inferred level of perceptual learning. If perceptual learning has retuned the neurons representing certain orientations in V1, for example, then transfer to a nearby but different orientation should be difficult, and retesting of the original orientation after new training on a second orientation should show alteration in performance. However, two apparently conflicting sets of targets can sometimes be learned either successively or simultaneously without significant interference. This implies that, although the relevant stimulus features may be coded early in visual system, learning may consist of changes in connectivity from the output of those early areas to an interaction structure or to a decision structure (Dosher and Lu, 1998; Dosher and Lu, 1999).

II. MECHANISMS OF PERCEPTUAL LEARNING

A converging methodology for the investigation of perceptual learning characterizes the limitations in performance of the observer and then identifies the aspects of performance that have improved with practice or training. Observer models and external noise tests are useful for this purpose. They allow the characterization of the dependence of perceptual performance in zero noise (absolute threshold) and in relation to limits on performance from high external noise in the stimulus. Improvements in performance can then be classified as stimulus enhancement improvements in zero or low noise or as external noise exclusion when the system is retuned to exclude limiting external noise.

A. Observer Models

Perceptual performance is limited by such factors as intrinsic stimulus variability, receptor sampling errors, randomness of neural responses, and loss of information during neural transmission. At an overall system level, these inefficiencies can be quantified in terms of a noisy ideal observer limited by *equivalent* internal noise—random internal noise necessary to produce the degree of inefficiency exhibited by the perceptual system (e.g., Lu and Dosher, 1999; Pelli, 1981). The amount of *equivalent* internal noise is estimated by systematically manipulating the amount of *external* noise (like TV snow or auditory white noise) added to the signal stimulus and observing how threshold—signal stimulus energy required for an observer to maintain a given performance level—depends on the amount of external noise (see Lu and Dosher, 1999 for a review). These methods characterize the overall limitations of the perceptual system, and allow comparisons of the

efficiency of the perceptual system in different perceptual tasks. In fact, specification of internal noise has become a requirement of any computational model of human perception (Sperling, 1989).

The noisy perceptual template model (PTM) (Lu and Dosher, 1999) includes (1) a perceptual template with signal stimulus with gain β; (2) a power function nonlinearity γ; (3) an multiplicative internal noise N_{mult} that is proportional to the energy in the stimulus; (4) an additive internal noise N_{add}, that accounts for absolute threshold; and finally, (5) a decision process that operates on the noisy internal representation of the stimulus. The amount of noise in the external stimulus is N_{ext}.

This model leads to a fundamental signal to noise equation for the observer system with three possible mechanisms of learning:

$$d' = \frac{(\beta c)'}{\sqrt{A_f^{2\gamma} N_{ext}^{2\gamma} + A_m^2 N_{mult}^2 \left((\beta c)^{2\gamma} + A_f^{2\gamma} N_{ext}^{2\gamma}\right) + A_a^2 N_{add}^2}}$$

The three learning improvement factors are A_f ($0 \leq A_f \leq 1$), which reduces external noise N_{ext}, A_a ($0 \leq A_a \leq 1$), which reduces internal additive noise N_a, and A_m ($0 \leq A_m \leq 1$), which reduces internal multiplicative noise N_m. This equation is rewritten to give the contrast threshold for a criterion d':

$$c_\tau = \frac{1}{\beta}\left[\frac{\left(1 + A_m^2 N_{mult}^2\right)\left(A_f N_{ext}\right)^{2\gamma} + \left(A_2^2 N_{add}^2\right)}{1/d'^2 - A_m^2 N_m^2}\right]^{\frac{1}{2\gamma}}$$

The PTM observer model, its relation to earlier linear observer models, and tests for mechanism mixtures (Lu and Dosher, 1999), are described in more detail in chapter 79, which develops the mechanisms of attention within the same framework.

B. Mechanism Signatures

There are three distinct mechanisms of perceptual learning: *stimulus enhancement*, *external noise exclusion*, and changes in *gain control*. These mechanisms are analogous to three aspects of signal processing: amplification, filtering, and gain control modification. Each of the three mechanisms has a key signature in perceptual task performance.

Learning through external noise exclusion is seen as improvement (A_f) in the ability to filter out external noise added to the stimulus, resulting in reduced thresholds in high external noise. It reflects learning to focus on the appropriate time, spatial region, and/or feature content of the signal stimulus. Learning through stimulus enhancement is seen as improvement (A_a) in the amplification of the stimulus,

resulting in reduced thresholds in zero or low external noise (e.g., absolute threshold). Learning through multiplicative noise reduction or through a change in nonlinear transducer are learning-induced changes (A_m) in gain control, would be seen in all external noise conditions.

Changes in external noise exclusion and in stimulus enhancement both show effects that are the same (on a log scale of performance) regardless of the criterion performance level used to define threshold, c_τ. Changes in gain control, and specifically in multiplicative internal noise, lead to effects that appear larger (on a log scale) at higher criterion performance levels (Dosher and Lu, 1999). To date, changes in gain control due to perceptual learning have not been observed, but both isolated cases of external noise exclusion and mixtures of external noise exclusion and stimulus enhancement have been observed in perceptual learning.

C. Observed Mechanisms

Perceptual learning may improve external noise exclusion (filtering), stimulus enhancement (amplification), or both. When both forms of improvement occur, one mechanism of learning may be more effective than the other. Consider several examples.

Figure 78.1 shows an example (Dosher and Lu, 1998; Dosher and Lu, 1999) in which both mechanisms of learning are prominent, although the magnitudes are partially decoupled. Performance in an orientation discrimination task in visual periphery was dramatically improved with practice. Figure 78.1a shows the spatial layout of the stimulus, which used a dual-task format: the character 5/S was discriminated in a rapid stream of characters at fovea, whereas the orientation (top tilted ±12 deg from vertical) of a small sine wave patch (Gabor) was discriminated in the periphery. Contrast thresholds were measured using two different adaptive staircases (see Figs. 78.1b and c) yielding 70.3% and 70.7% accuracies. Performance was measured in a range of external noise conditions (see Fig. 78.1d).

The threshold signal contrasts depend upon criterion accuracy, external noise level, and practice (see Fig. 78.1e). Higher criterion accuracy demands higher contrast thresholds. In the high-noise region where external noise is the limiting factor in performance, contrast thresholds increase with increasing external noise. Practice reduces contrast thresholds by a downward vertical shift (in the log) with practice in both zero and in high external noise (albeit with slightly different magnitudes). We also observed a shift relationship between thresholds at the two performance criteria. These strong shift properties in the log
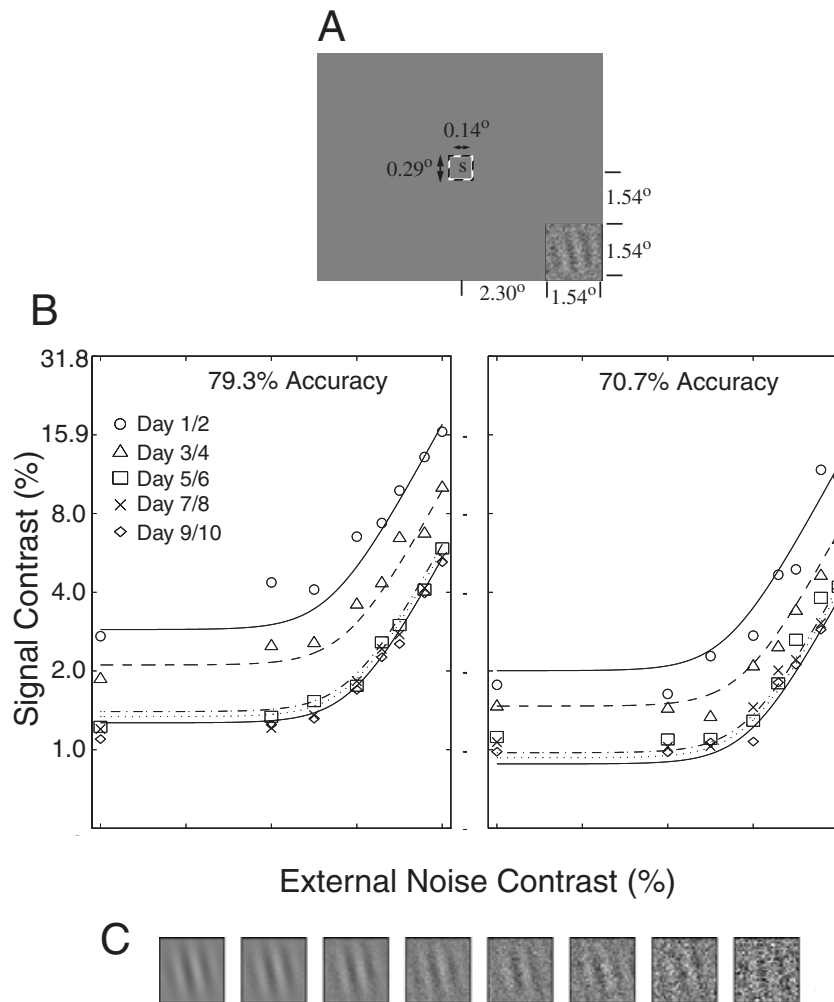
FIGURE 78.1   A perceptual learning task using the external noise paradigm. **A.** Spatial layout of the task, including the peripheral orientation discrimination Gabor stimulus, and a central letter stimulus for a secondary task. **B.** Contrast threshold (Gabor signal contrast corresponding to the criterion accuracy) as a function of the external noise in the stimulus. Threshold is a systematic function of criterion, external noise, and practice (data from Dosher and Lu, 1998). **C.** Examples of a signal of constant contrast embedded in increasing amounts of external noise.

contrast threshold as a function of criterion are a special characteristic of the perceptual template model. These results were subsequently replicated in face and in texture identification tasks (Gold, Bennett, and Sekuler, 1999).

Other studies using the external noise paradigm and framework have clearly documented the independence of these two mechanisms of learning in high and low external noise. For example, in certain conditions, such as training orientation discrimination in fovea, external noise exclusion is isolated as a separate mechanism. Figure 78.2 illustrates the results of practice in an orientation discrimination task at the fovea. Oriented sinewave patches (Gabors) of 45° ± 8° were

discriminated (Lu and Dosher, submitted). This result is important because it isolates learning to exclude high external noise as distinct from enhancement of the stimulus. This rules out explanations of perceptual learning as an improvement in calculation efficiency.

D. Attention in Perceptual Learning

Many behavioral tests of perceptual learning in vision require the observer to maintain fixation while carrying out the critical perceptual task(s) in the periphery. Sometimes (Dosher and Lu, 1998; Karni and Sagi, 1991), fixation is ensured by the presence of a task at fovea. This requires the division of perceptual
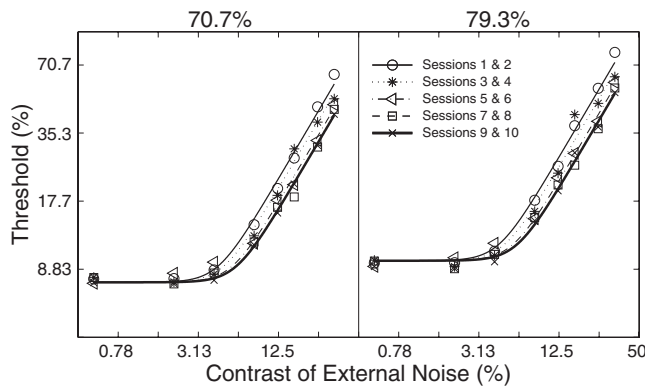
FIGURE 78.2 Perceptual learning in fovea that isolates external noise exclusion, reflecting learning about when, where, and what to look for in the target stimulus. These data (Lu and Dosher, submitted) measured the threshold signal contrast to discriminate the orientation (45° ± 8°) of a sine wave patch at fovea at two different performance criteria.

resources across the task at fixation and the task in the periphery, and/or division between overt direction of the eye and attention. The importance of learning to attend to the perceptual task, especially when this involves sharing resources between fovea and periphery, deserves further systematic investigation. Even in cases where fixation and perception are not divided, learning has been reported to be restricted to the relevant or attended feature of a perceptual stimulus (Ahissar and Hochstein, 1998), whereas irrelevant variations that later become the aspect to be judged may benefit little if at all from exposure to variation in an irrelevant feature. Alternatively, some researchers have claimed that perceptual sensitivity is improved by practice even when the relevant stimuli are subliminal adjuncts to the primary task, although learning of unattended stimuli appears to require correlation with an attended task (Seitz and Watanabe, 2003).

III. RETUNING VERSUS REWEIGHTING

Visual perceptual learning may reflect plasticity in early visual areas that alters the basic sensory coding of the stimulus (Karni and Sagi, 1991) or it may reflect plasticity of the connections between the sensory coding of the stimulus and decision units that may reside at higher cortical levels (Dosher and Lu, 1998; Mollon and Danilova, 1996). If retinal or stimulus feature specificity is demonstrated, then this implicates the selection of early visual representations in the connections to decision, but it does not require that early visual representations be altered by training. Plasticity
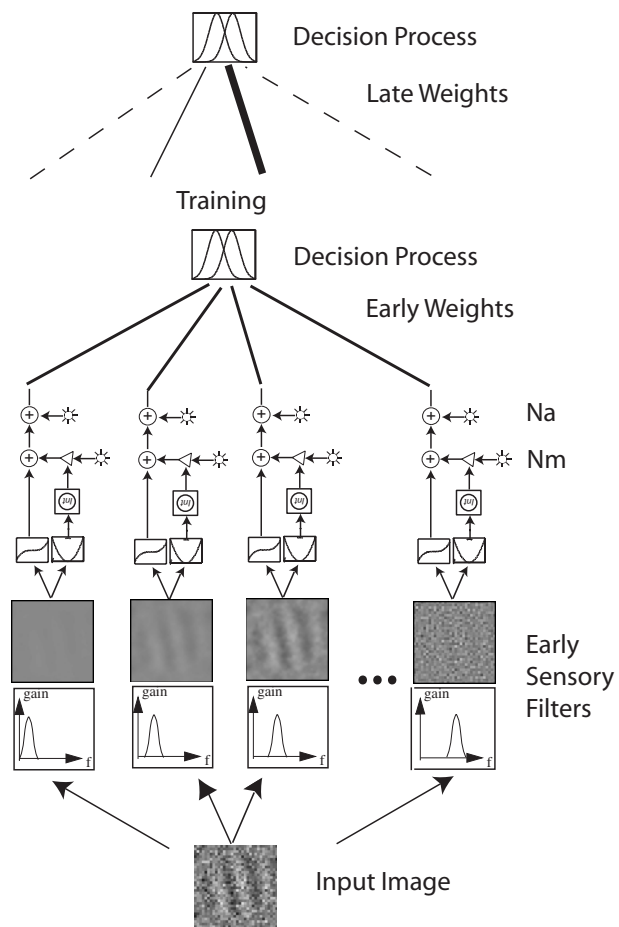

FIGURE 78.3 Schematic diagram of the perceptual system and perceptual learning via reweighting. The visual input is represented in early sensory filters, and this information is then fed to decision units. Perceptual learning that is specific to an attribute of early sensory filters (e.g., location, orientation, scale) may reflect retuning of the sensory representation (not shown), or a constant sensory representation with changes in the feed-forward weights to decision.

based on reweighting has the additional advantage that early visual representations are left unchanged, so that perceptual learning of one task need not impact on another task and is hence compatible with observed abilities for compatible training of multiple perceptual tasks.

A schematic of reweighting due to practice is shown in Fig. 78.3. Early sensory filters specified for different spatial frequencies (and orientations) improve their connections to decision without changing the properties of the filters themselves. Perceptual learning may consist in learning optimal weights for inputs from early sensory coding. Network models are beginning to be developed to account for perceptual learning in specific tasks (Fahle and Poggio, 2002).

IV. PHYSIOLOGICAL CORRELATES OF LEARNING

Alteration of early sensory representations through training or exposure has been widely reported in auditory (Bakin and Weinberger, 1990) and somatosensory cortex (Recanzone, Merzenich, Jenkins, Grajski, and Dinse, 1992). In these cases, repeated experience with certain stimuli causes either narrowed tuning of the early cortical cells, or recruited additional cells into responding to the trained stimuli.

In the case of visual perceptual learning, however, evidence for substantial alterations in early visual cortices with training or practice is lacking. In three separate studies (Crist, Li, and Gilbert, 2001; Ghose, Yang, and Maunsell, 2002; Schoups, Vogels, Qian, and Orban, 2001) in awake behaving monkeys, behavioural performance has improved significantly, these improvements are to some degree specific, yet there is little (Schoups et al., 2001) or no (Crist et al., 2001; Ghose et al., 2002) evidence for significant changes in tuning of cells in V1 or V2. These results suggest that, minimally, perceptual learning must involve plasticity at many levels, certainly at a range of levels above V1 and V2. On the other hand, location and orientation specificity of learning identifies these early visual areas as the locus of the relevant sensory representations that are read-out to higher levels.

A combined analysis and correlation of physiological evidence, sophisticated behavioral analysis—including observer models and external noise tests—and explicit (network) models of the learning process in future developments will allow a full specification of perceptual learning at the neural and the behavioural levels.

V. IMPACT OF PERCEPTUAL LEARNING

The mechanisms of perceptual learning have wide ranging implications for the nature of plasticity in adult systems. The existence of perceptual learning also has possible practical implications for many technical areas of assisted perception and recovery from injury or damage. For example, perceptual learning processes can be very important following the introduction of hearing aids or cochlear implants. Technological environments with assisted perception displays may require training and perceptual learning to support optimized performance. How to optimize perceptual learning remains an important question for many practical applications.

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