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Neurobiology of Learning and Memory

Visual perceptual learning

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ABSTRACT

Perceptual learning refers to the phenomenon that practice or training in perceptual tasks often substantially improves perceptual performance. Often exhibiting stimulus or task specificities, perceptual learning differs from learning in the cognitive or motor domains. Research on perceptual learning reveals important plasticity in adult perceptual systems, and as well as the limitations in the information processing of the human observer. In this article, we review the behavioral results, mechanisms, physiological basis, computational models, and applications of visual perceptual learning.

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1. Introduction

Although early Gestalt psychologists denied any role of learning in perception, Helmholtz (1911) made learning an essential component in his theories of perception. Taking an ecological approach, Gibson (1967) reviewed development of perceptual expertise in early childhood and postulated that perceptual learning is a process of discovering how to transform previously overlooked potentials of sensory stimulation into effective information. The systematic documentation of various specificities of perceptual learning with implications of an early sensory site of learning recharged the research on perceptual learning (Karni & Sagi, 1991). Since then, perceptual learning in adult human observers has been documented in a wide range of perceptual tasks in visual, auditory, and somato-sensory domains (Fahle & Poggio, 2002). In this review, we focus on perceptual learning in the visual domain.

2. Perceptual learning

Perceptual learning has been documented in virtually every visual task, including the detection or discrimination of visual gratings (DeValois, 1977; Fiorentini & Berardi, 1980, 1981; Mayer, 1983), stimulus orientation judgment (Dosher & Lu, 1998; Shiu & Pashler, 1992; Vogels & Orban, 1985), motion direction discrimination (Ball & Sekuler, 1982, 1987; Ball, Sekuler, & Machamer, 1983), texture discrimination (Ahissar & Hochstein, 1996; Karni & Sagi, 1991, 1993), time to perceive random dot stereograms (Ramachandran & Braddick, 1973), stereoacuity (Fendick & Westheimer, 1983), hyperacuity and vernier tasks (Beard, Levi, & Reich, 1995; Bennett & Westheimer, 1991; Fahle & Edelman, 1993; Kumar & Glaser, 1993; McKee & Westheimer, 1978; Saarinen & Levi, 1995), and object recognition (Furmanski & Engel, 2000).

The trade-mark finding in perceptual learning is that some of what is learned is specific to stimulus or task factors such as retinal location (Karni & Sagi, 1991), spatial frequency (Fiorentini & Berardi, 1980), orientation (Poggio, Fahle, & Edelman, 1992) (Fig. 1), or background texture (Ahissar & Hochstein, 1996). Perceptual learning that is highly specific to retinal location and stimulus has been claimed to reflect neural plasticity in basic visual processing mechanisms (Karni & Sagi, 1991).

Several recent papers re-examined specificity of perceptual learning and found that a number of factors in the training procedures, some of that were not obviously related to specificity or transfer of learning, determine the degree of specificity, including task precision (Jeter, Dosher, Petrov, & Lu, 2009), task difficulty (Ahissar & Hochstein, 1997), number of trials (Censor & Sagi, 2009), and training schedule (Xiao et al., 2008). Xiao et al. (2008) developed a novel double-training paradigm that employed conventional feature training (e.g., contrast) at one location, and additional training with an irrelevant feature/task (e.g., orientation) at a second location, either simultaneously or at a different time. They showed that this additional location training enabled a complete transfer of feature learning (e.g., contrast) to the second location. Understanding factors that determine specificity/transfer of perceptual learning is one of the most important challenges in the study of perceptual learning.

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Fig. 1. Effect of switching from vertical to horizontal verniers (or vice versa) after block 20. Averaged results of 12 naïve subjects; six started with horizontal verneiers, and the others stated with vertical verniers. There is no transfer of learning. (After Poggio et al. (1992)).

3. Mechanisms of learning

Mechanisms of perceptual learning, i.e., what is learned during perceptual learning, have been investigated in recent years in psychophysics (Dosher & Lu, 1998, 1999; Gold, Bennett, & Sekuler, 1999; Saarinen & Levi, 1995), neurophysiology (Crist, Li, & Gilbert, 2001; Ghose, Yang, & Maunsell, 2002; Schoups, Vogels, Qian, & Orban, 2001), brain imaging (Schiltz et al., 1999; Schwartz, Maquet, & Frith, 2002), and patients (Fahle & Daum, 2002; Xu et al., 2010).

In psychophysical studies, Dosher and Lu (1998) introduced a theoretical framework and an external noise plus training paradigm to analyze how perceptual inefficiencies improve over the course of perceptual learning (Fig. 2). Perceptual inefficiencies are attributed to three limitations in perceptual processes (Lu & Dosher, 2008): an imperfect perceptual template, internal additive noise, and multiplicative noise. Systematic measurements of human performance as a function of both the amount of external
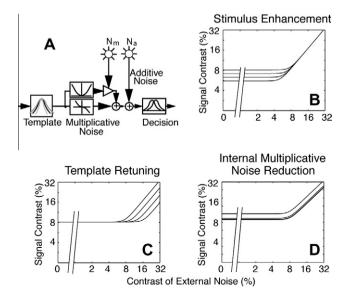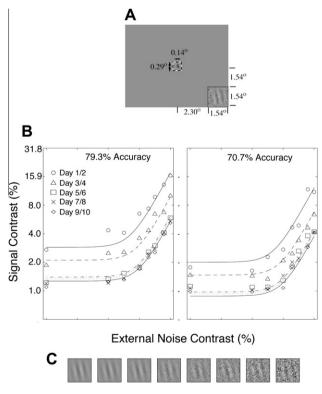
noise added to the signal stimulus and the length of training received by the observers make it possible to distinguish three mechanisms of perceptual learning: perceptual template retuning, stimulus enhancement, and contrast-gain control reduction. It has been consistently found that two independent mechanisms (Fig. 3), stimulus enhancement and external noise exclusion, support perceptual learning in a range of tasks (Dosher & Lu, 1998, 1999, 2005, 2007; Lu, Chu, & Dosher, 2006; Lu & Dosher, 2004).

Although practice-induced neuronal plasticity has been documented in auditory (Metherate & Weinberger, 1990; Weinberger, Javid, & Lepan, 1993) and somato-sensory cortices (Jenkins, Merzenich, Ochs, Allard, & Guic-Robles, 1990; Recanzone, Merzenich, & Schreiner, 1992), and in some visual fMRI studies (Schiltz et al., 1999; Schwartz et al., 2002; Vaina, Belliveau, des Roziers, & Zeffiro, 1998), evidence for practice-induced neuronal plasticity in early visual cortical areas is however modest (Crist et al., 2001; Ghose et al., 2002; Schoups et al., 2001; Yang & Maunsell, 2004), although neurons in V1 may exhibit task specific tuning (Li, Piech, & Gilbert, 2004) that seem to reflect selection of task-relevant stimulus features for a particular task rather than persistent cross-task changes in neuronal tuning. Law and Gold (2008) found that perceptual learning in motion direction discrimination does not involve neuronal response changes in the middle temporal area (MT), but rather in the lateral intraparietal area (LIP), a brain area related to selective readout of MT neurons. They conclude, "...[our] results suggest that the perceptual improvements corresponded to an increasingly selective readout of highly sensitive MT neurons by a decision process, represented in LIP, that instructed the behavioral response." In sum, these reports found that early visual representations showed either no change or

Fig. 3. 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.

Fig. 2. The perceptual template model (PTM) and the signatures of three mechanisms of perceptual learning. (After Dosher and Lu (1998)).
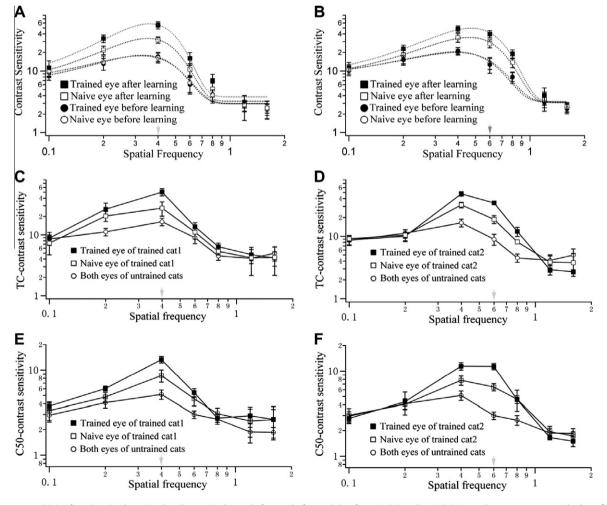
modest changes in the slopes of tuning functions following perceptual learning.

One critical difference between existing neurophysiological investigations of perceptual learning contrasting cortical plasticity in auditory and somato-sensory domains, which exhibit strong plasticity, and that in the visual domain, where evidence for early visual plasticity is modest, lies in the animal specifies: non-primates are used in the auditory and somato-sensory domains, whereas primates are used in the visual domain. It's possible that primates exhibit less training-induced plasticity than non-primates in early visual areas (Karmarkar & Dan, 2006; Yao, Shi, Han, Gao, & Dan, 2007).

Some recent evidence might suggest greater plasticity in early visual areas occurs in non-primates. Hua et al. (2010) examined the effects of training in grating orientation identification on both perceptual and neuronal contrast sensitivity functions of cats using combined psychophysical measurements with extracellular single-unit recording under anesthetized preparations. Conditioning was used to train cats to identify the orientation of a high contrast ±45° sinusoidal grating. Subsequently, the same procedure was used to measure monocular contrast sensitivity functions (CSF) in both eyes. The cats were then trained monocularly to perform a near-threshold orientation identification task. After approximately 40 days of training, monocular CSFs were measured again, followed by extracellular recordings of single-unit activities from the primary visual cortex (V1) of anesthetized cats. Contrast response functions to the preferred stimuli were measured for isolated neurons. The combined contrast sensitivities of individual neurons were then used to construct the neuronal CSFs for neuronal populations that responded preferentially to the stimuli presented via trained or untrained eyes (Fig. 4).

Hua et al. (2010) found that: (1) training improved perceptual contrast sensitivity, with some degree of specificity for the training spatial frequency and training eye, (2) training also improved the contrast sensitivity of V1 neurons responding preferentially to the trained spatial frequency, (3) perceptual and neuronal CSFs were highly correlated both before and after training, and (4) a systematic analysis of the parameters of the neuronal contrast response functions indicated that the learning-induced plasticity was caused by increased contrast-gain of the neurons associated with training. The increased contrast-gain resulted in a parallel leftward shift of the neuronal contrast response functions, consistent with decreased post-synaptic polarization (Carandini & Ferster, 1997; Ohzawa, Sclar, & Freeman, 1985; Sanchez-Vives, Nowak, & McCormick, 2000a, 2000b; Sclar, Lennie, & DePriest, 1989).

In addition to the difference in animal species, the Hua et al. (2010) study differs from previous neurophysiological studies on perceptual learning in two other ways: (1) previous electrophysiological studies exploring training-induced visual cortical plasticity generally used orientation threshold as the dependent measure.

Fig. 4. Contrast sensitivity functions in the trained and untrained eyes before and after training for cat1 (A) and cat2 (B). Smooth curves represent the best fitting Gauss functions. The green arrows indicate the trained spatial frequency, and the error bars represent 1 SD. (CD) TC-contrast sensitivity functions of V1 neurons recorded from cat1 (C) and cat2 (D). (EF) C_{50}-contrast sensitivity functions of V1 neurons recorded from cat1 (E) and cat2 (F). Green arrows indicate the trained spatial frequency. All values are displayed as mean ± SEM. (After Hua et al. (2010)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Hua et al. (2010) used contrast thresholds as the dependent measure. It is possible that different neural networks might be involved in orientation discrimination and contrast detection. (2) Hua et al. (2010) recorded the response of V1 neurons in anesthetized and paralysed cats, whereas previous studies made recordings in awake-behaving monkeys. Compared to studies on anesthetized cats, recordings from early visual cortical areas of wake monkeys may include substantial top-down influences from higher visual cortical areas (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Li, Levi, & Klein, 2004; Watanabe et al., 1998). New studies are necessary to further investigate all these factors.

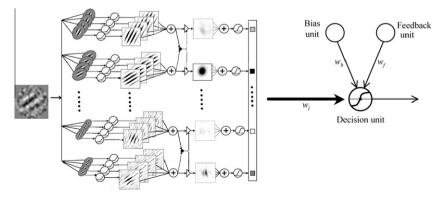## 4. The role of attention and feedback

Although earlier studies (Ahissar, Laiwand, Kozminsky, & Hochstein, 1998; Schoups et al., 2001; Shiu & Pashler, 1992) found that subjects can only learn the feature they paid attention to, recent studies by Watanabe and colleagues (Seitz & Watanabe, 2003; Watanabe, Nanez, & Sasaki, 2001; Watanabe et al., 2002) found that attention to a feature is not necessary for perceptual learning of the feature to occur if the feature is irrelevant to the primary task performed by the subject. Recent studies suggest that the performance improvement from task-irrelevant learning can be enhanced by attending to the feature (Gutnisky, Hansen, Iliescu, & Dragoi, 2009).

Another important topic in perceptual learning concerns the role of feedback. The empirical pattern of results is quite complex (see Dosher & Lu, 2009 for a review). Whereas most perceptual learning studies employed trial-by-trial feedback, several studies documented significant perceptual learning with block, partial, or even no feedback, and no perceptual learning with false, random, manipulated block, and reversed feedback (Herzog & Fahle, 1997). Shibata, Yamagishi, Ishii, and Kawato (2009) showed that arbitrary block-feedback facilitated perceptual learning if it is more positive than the observer's actual performance. At high training accuracies, training with and without feedback generated essentially the same learning curves (Liu, Lu, & Dosher, 2010b), and significant learning was found in low training accuracy trials when they were mixed with high accuracy trials (Liu, Lu, & Dosher, 2009; Petrov, Dosher, & Lu, 2006). Liu, Lu, and Dosher (2010a) conducted a computational analysis of the complex pattern of empirical results on the role of feedback with the Augmented Hebbian Reweighting Model (Petrov, Dosher, & Lu, 2005), including a study that showed significant perceptual learning with block, partial, or even no feedback, and no perceptual learning with false, random, manipulated block, and reversed feedback (Herzog & Fahle, 1997), another study (Shibata et al., 2009) that showed that arbi-

trary block-feedback facilitated perceptual learning if it is more positive than the observer's actual performance, and the interaction between feedback and training accuracy (Liu et al., 2010b). The simulation results are both qualitatively and quantitatively consistent with the data reported in the literature.

5. Computational models

One major open question is whether perceptual learning reflects representation enhancement in early sensory areas or reweighting of sensory representation in the decision process. Petrov, Dosher, and Lu (2005) introduced a task analysis framework to evaluate the diagnostic value of experimental designs for discriminating reweighting and representational enhancement in perceptual learning. A systematic review of the literature suggests that the two potential forms of plasticity – reweighting versus representational change – make similar predictions about specificity in most of the existing studies that had previously been cited as evidence for representational enhancement.

A number of models have been proposed in perceptual learning (Herzog & Fahle, 1998; Petrov et al., 2005, 2006; Vaina, Sundareswaran, & Harris, 1995; Vallabha & McClelland, 2007; Weiss, Edelman, & Fahle, 1993; Zhaoping, Herzog, & Dayan, 2003) (see Tsodyks & Gilbert, 2004, for a review). All these models assume an appropriate stimulus representation and postulate incremental learning; none proposes systematic changes in representation. Based on the results from the task analysis and neurophysiology, Petrov et al. (2005, 2006) implemented the reweighting hypothesis outlined in Dosher and Lu (1998) in a multi-channel Augmented Hebbian Reweighting Model (AHRM) (Fig. 5). The AHRM consists of four units: representation units that encode input images as activation patterns, a task-specific decision unit that receives weighted inputs from the representation units, an adaptive *bias unit* that accumulates a running average of the response frequencies and works to balance the frequency of the two responses, and a *feedback unit* that makes use of external feedback when (and if) it is presented. Learning in the model occurs exclusively through incremental Hebbian modification of the weights between representation units and the decision unit; while the early processing pathway that constructs representations from the retinal image remains fixed throughout training. The AHRM has been very successful in modelling a wide range of phenomena in perceptual learning, including complex patterns of perceptual learning in an orientation discrimination experiment under destabilizing non-stationary manipulations both with and without trial-to-trial feedback (Petrov et al., 2005, 2006), a large number of data patterns in

Fig. 5. Augmented Hebbian Reweighting Model (AHRM, Petrov et al., 2005) passes stimulus images through a *representational system* of orientation and spatial-frequency tuned units, with non-linearities and spatial pooling. These activations, along with inputs to a bias and feedback unit are weighted by the *task-specific weighting system* to yield a decision. The AHRM has predicted the dynamics of learning in non-stationary training, the various roles of feedback in learning, and performance in external noise paradigms. (After Petrov et al. (2005)).

external noise studies of perceptual learning (Lu, Liu, & Dosher, 2010), and the complex patterns of results on the role of feedback in perceptual learning (Liu et al., 2010a).
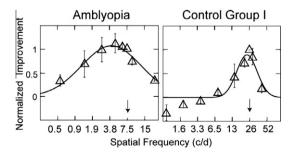
6. Applications

The remarkable levels of neural plasticity and neurogenesis in the adult nervous system (Bruel-Jungerman, Davis, & Laroche, 2007; Gould, 2007; Johansson, 2007; Kramer & Erickson, 2007) have led to the test and development of visual rehabilitation programs based on perceptual learning. Here we discuss one example application of perceptual learning in treating amblyopia.

Amblyopia is a developmental spatial vision impairment that cannot be corrected by refractive means. It affects about 3% of the population (Ciuffreda, Levi, & Selenow, 1991; McKee, Levi, & Movshon, 2003; Simmers, Ledgeway, Hess, & McGraw, 2003). Conventional wisdom on visual development suggests that spatial vision becomes hard-wired after a critical period, usually around 6–8 years of age (Berardi, Pizzorusso, Ratto, & Maffei, 2003); The amblyopic visual system is generally thought to be fully (though erroneously) developed by age eight and therefore no longer subject to therapeutic modifications. In clinical practice, only infant and young child amblyopes are treated, while patients older than 8 years are left untreated (Greenwald & Parks, 1999).

Exploiting neural plasticity in the adult visual system, several laboratories have demonstrated that perceptual training can be used in the adult amblyopic visual system for visual rehabilitation (Chung, Li, & Levi, 2006; Levi & Polat, 1996; Li & Levi, 2004; Li et al., 2004a; Li, Provost, & Levi, 2007; Polat, Ma-Naim, Belkin, & Sagi, 2004; Zhou et al., 2006). One critical concern is the efficiency of such treatment. Because the hallmark of perceptual learning in the normal visual system is its specificity to the characteristics of the training stimulus (Fahle, 2002), there is a question about generalizability of such training. If perceptual learning in the amblyopic visual system were also highly specific to the characteristics of the training stimuli and task, perceptual learning as a therapy for amblyopia would not be very effective in improving general spatial vision. At a minimum, multiple training stimuli and tasks would need to be used to cover the range of stimuli and tasks important for daily visual functions.

To evaluate and compare the generalizability of perceptual learning in amblyopic and normal vision, (Huang, Zhou, & Lu, 2008) estimated the bandwidth of perceptual learning in both normals and amblyopes. They found that the bandwidth of perceptual learning was drastically different ($p < 0.01$): for the amblyopic observers, the average full bandwidth was 4.04 ± 0.63 octaves;

the average full bandwidth was only 1.40 ± 0.30 octaves for the normal observers (Fig. 6). The estimated 4.04 octaves bandwidth of perceptual learning implies that the impact of perceptual learning generalizes across spatial frequency channels in amblyopic eyes. Such a broad bandwidth of perceptual learning may underlie the improved visual acuity in the amblyopic eyes following training, a task that involves a wide range of spatial frequencies.

7. Conclusion

The susceptibility of the adult visual system to training suggests that the perceptual system is not static even in adulthood. We cannot fully understand perception without understanding perceptual learning. Research on perceptual learning is of theoretical significance in illuminating plasticity in adult perceptual systems, and in understanding the limitations in the information processing of the human observer. It is of practical significance as a potential method for the development of perceptual expertise in normal populations and for the non-invasive amelioration of deficits in challenged populations by training.

Acknowledgments

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Fig. 6. Average contrast sensitivity improvements as functions of spatial frequency for the amblyopic (a) and first control groups (b). The magnitudes of contrast sensitivity improvements were normalized to that at the training spatial frequency; spatial frequencies were normalized to the training frequency. Blue arrows indicate the average training spatial frequency. Data were weighted by their standard deviation. Only observers with significant contrast sensitivity improvements during training are included. Error bars indicate SEM. (After Huang et al. (2008)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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