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Perceptual learning: specificity versus generalization

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Perceptual learning improves performance on many tasks, from orientation discrimination to the identification of faces. Although conventional wisdom considered sensory cortices as hard-wired, the specificity of improvement achieved through perceptual learning indicates an involvement of early sensory cortices. These cortices might be more plastic than previously assumed, and both sum-potential and single cell recordings indeed demonstrate plasticity of neuronal responses of these sensory cortices. However, for learning to be optimally useful, it must generalize to other tasks. Further research on perceptual learning should therefore, in my opinion, investigate first, the conditions for generalization of training-induced improvement, second, its use for teaching and rehabilitation, and third, its dependence on pharmacological agents.

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Current Opinion in Neurobiology 2005, 15:154–160

This review comes from a themed issue on
Cognitive neuroscience
Edited by Angela D Friederici and Leslie G Ungerleider

Available online 23rd March 2005

0959-4388/\$ – see front matter

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DOI 10.1016/j.conb.2005.03.010

Introduction: perceptual learning

Perceptual learning (PL) is defined as a change of performance, usually an improvement, as a result of training. The improvement tends to persist over weeks and months, distinguishing it from sensitization, habituation and priming (see glossary) that all show more transient changes in performance. Perceptual learning is often quite specific for the exact task trained and does not lead to conscious insights that can be easily communicated; hence, it is of the procedural or implicit type. Many forms of PL change the cortical circuits solving the perceptual task trained, unlike episodic and factual memory, which seem to be stored in brain areas that are not directly involved in the analysis of the sensory signals.

The past couple of years, covered by this review, saw increased activity in the field of PL as is evident from the

volume of published material (several hundred publications) that has appeared on this topic during that time. One important topic is the question of how specific the improvement achieved through learning is, and how much it can generalize (see glossary). This question is closely related to the question of what cortical changes underlie the behavioral improvement. Given the fact that ‘early’ stages of processing tend to be more specific for low level features such as position and orientation of a stimulus, a high specificity of PL, that is, a low degree of transfer to other orientations or positions fits better with a neuronal substrate at early cortical levels. Generalization of improvement across different stimulus positions and orientations, conversely, is more compatible with a higher level of neuronal plasticity, because these levels tend to generalize over stimulus position and orientation. Because it is notoriously difficult to pinpoint the location of neuronal changes by means of psychophysical experiments, the results of electrophysiological and imaging studies are reviewed wherever such studies are available.

The results show an involvement of early sensory cortices in PL and indicate the important role of feedback connections from ‘higher’ to ‘lower’ levels of processing. The next steps will be to gain a better understanding of under which training conditions improvement generalizes, can be used for visual rehabilitation, and might be influenced pharmacologically. In this review, recent psychophysical, electrophysiological, pharmacological and computational studies of perceptual learning are reviewed with special emphasis on the dichotomy between specificity and generalization of improvement.

Reviews on perceptual learning

The vitality of the PL field is mirrored not only in the large number of original articles but also in several reviews dealing with different aspects of PL. The most comprehensive summary of PL up to 2002 is to be found in Fahle and Poggio [1]; the introduction of the book reviews the literature up to that year. Unfortunately, there are often large differences both between the results of different studies and between individuals [2]. In order to make comparisons across different studies, improvement based on training was converted to a common measure, d' . It transpires that several factors, such as task complexity, strongly affect the speed of PL [3].

The reverse hierarchy theory of PL (see glossary) outlines a general framework for perceptual learning on different neuronal levels. The theory assumes that learning starts at high cortical areas (where it generalizes) and progresses backwards towards lower levels if necessary (where it is

Glossary

Amblyopes: Patients suffering from a, sometimes strongly, reduced visual acuity even after complete correction of refractive errors, and despite having a normal retina and optic nerve. Often, amblyopia is caused by a squint, with one eye effectively 'switched off' during infancy and childhood.

Early selection theory: The hypothesis that in PL irrelevant signals should be eliminated as early as possible during cortical information processing. Hence PL might change processing at rather 'early' stages of cortical signal processing, in analogy to the early selection theory of attention.

Gabor-patch: Usually a small round patch with blurred edges, containing a sinewave grating, that is, a pattern of blurred stripes.

Generalization: The transfer of an improvement achieved through training to other similar stimuli. The improvement generalizes to the new stimuli.

Habituation: A special case of adaptation, namely, a shift of sensitivity (working range of the sensory system) towards lower levels, as in the case of a less pronounced reflex response after prolonged stimulation. (This is the opposite of sensitisation.)

Late selection theory: The hypothesis that in PL irrelevant signals should be eliminated at a relatively late stage of cortical information processing, leaving peripheral cortices unchanged. According to this theory, PL mainly relies on selection of the most suitable signals at late stages of cortical signal processing, in analogy to the late selection theory of attention.

Non-words: Strings of (ordinary) letters that do not form (English) words.

Orientation bandwidth (halfwidth): The difference in stimulus orientation required for an effect to decrease to half its strength. For example, if an observer adapts to a grating stimulus, the orientation halfwidth indicates how much the grating has to be rotated in order for the adaptation to decrease to half of its strength at the adapted orientation.

Priming: The effect of a (sometimes very faint) preceding stimulus on the reception and perception of another stimulus, usually presented with temporal proximity.

Reverse hierarchy theory of PL: The theory that easy conditions guide the learning of difficult ones. Improvement begins at higher cortical levels and proceeds to lower-levels if necessary. The theory was originally proposed by Ahissar and Hochstein [64].

Sensitisation: A transient increase in sensitivity as a result of stimulation, for example lower thresholds for pain shortly after a painful stimulus. (This is the opposite of habituation.)

Sum potentials: Electric or magnetic potentials that can be recorded outside the skull, representing the joint (and synchronized) activity of large neuronal networks in the brain. Examples are the EEG and event related potentials (ERP).

Visual span: The range around the center of gaze where letters are recognized. Visual span profiles plot the accuracy of letter recognition as a function of horizontal distance from the midline.

specific). A recent review by Ahissar and Hochstein summarizes evidence supporting this theory [4]. A slightly different view contrasts an early selection theory (see glossary) of PL with a late selection theory (see glossary), in analogy to theories on attention, and argues that selection should occur as early as possible to optimize the signal-to-noise ratio [5]. In this respect, perceptual and motor learning are similar and might both rely on changes in neuronal tuning functions [6]. Generalization is at the heart of useful learning in both systems [7], and apparently relies on strong top-down influences [8]. The neuronal correlate of PL is best investigated by electrophysiological studies, as reviewed by Ghose [9].

The consensus seems to be that PL occurs at different processing levels, with different speeds, and is subject to top-down influences. The specificity of learning might differ among sensory modalities, so a discussion themed by modality appears to be the most appropriate way to approach the subject.

Perceptual learning in the visual domain: specificity

A prominent aspect of PL that is studied in psychophysical experiments is the specificity of the improvement on stimulus orientation. The orientation bandwidth (see glossary) of orientation selective mechanisms and their improvement as a result of training is investigated by rotating a stimulus after the training phase and by testing the amount of transfer to other stimulus orientations [10[•]]. The orientation specificity of PL certainly is much smaller than the bandwidth of early orientation-selective filters, which serves as another argument for top-down influences shaping the peripheral filters in a task-dependent way [5].

Even luminance contrast detection improves through training, and generalizes across orientations. This finding is surprising given the fact that humans should be over-trained for contrast detection through everyday life, especially under low illuminances [11]. Obviously, training of some tasks is orientation-specific, whereas generalization occurs in others.

PL is specific for several hitherto not or rarely examined stimulus parameters, such as motion-speed and motion-direction [12]. Motion discrimination improves even with 'paired-dots' stimuli that are supposed not to activate cortical middle temporal area (MT) [13]. Improvement of observers training on a shape discrimination task based on luminance contrast transfers to the detection of a shape defined by temporal structure, whereas it does not the other way round [14], and improvement with a visually masked stimulus is specific for the mask [15].

Perceptual learning in the visual domain: generalization and context

Often, improvement achieved through PL generalizes more for complex tasks than for simpler ones. Playing action video games indeed seems to generalize to other tasks [16[•]], and in visual search, both specific features and a global search strategy are learned [17]. Visual training through reading text seems to modify the way people perceive printed words: reading-related training improves perception of words but not of non-words (see glossary) [18]. Moreover, the size of the visual span (see glossary) expands through training, with an associated increase in maximum reading speed [19[•]]. These results encourage the use of PL in visual rehabilitation.

There is a controversy regarding the importance of context on PL. Initially, evidence indicated that detection of

a Gabor patch (see glossary) improved by practicing specifically in the presence of similar patches placed laterally [20,21]. However, learning and improvement on a task can occur without the stimulus being in the specific task context [22^{*}]. These results enable insights into the organization of visual perception; generalization of improvement indicates that different tasks employ at least partly identical neuronal mechanisms.

Perceptual learning in the visual domain: physiology

More than ten years ago, a study [23] found changes in early event-related sum potentials (see glossary) of humans as a result of PL, and several others corroborated the basic finding of training-induced changes in evoked potentials [24,25].

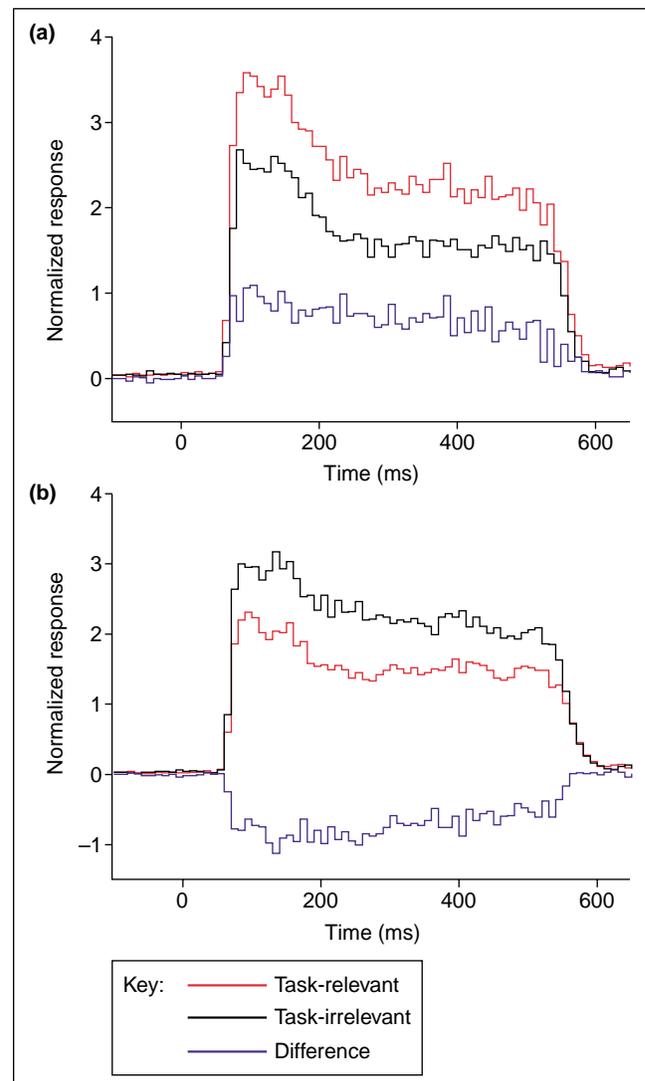
Training on an orientation discrimination task surprisingly decreases the number of neurons that represent the trained orientation in primary visual cortex (V1) of monkeys, without any evident changes in receptive field properties [9]. However, neurons in V4 with receptive fields in the trained region of the visual field narrow their orientation tuning and increase responses as a result of training [26]. Moreover, neurons in V1 change not only their contextual influences but also their classical receptive field properties depending on the animal's actual task, optimizing the information on the relevant stimulus feature under top-down influence (Figure 1; [27^{**}]). Similarly, neurons in infero-temporal cortex can show target selective neuronal responses during visual search [28].

Neurons in V4 respond more vigorously to noisy images the monkey had been trained with than to untrained images containing the same amount of noise [29^{*}]. Hence, training improves both perception and single cell responses that are noise-specific. In humans, training of visual texture discrimination increases activity in the corresponding quadrant of the visual field representation in V1 as demonstrated by fMRI [30].

Learning in audition, in somatosensation and in olfaction

The fast improvement with training not only in visual but also auditory tasks is, at least in tone frequency discrimination, mostly because of perceptual learning, and only marginally because of procedural learning of the task [31]. Discrimination of temporal intervals is relatively specific for interval length, but generalizes to other spectral frequencies [32]. Similar to the situation in the visual system, noise is eliminated at an early level; hence loss of efferent feedback (to the cochlea) degrades auditory perception in noise [33]. Extensive learning of the discrimination between 'r' and 'l' by native Japanese speakers activates several cortical and subcortical areas, indicative of modified sensory-motor connections [34,35].

Figure 1



The population response of neurons in monkey area V1 to identical stimuli. Normalized and averaged post-stimulus time histograms showing the time course of induced activation when the stimulus was task relevant versus when it was not. The difference between task relevant and task-irrelevant responses could be both positive (a) and negative (b), but it always started with the response proper. (Used with permission from Nature Publishing Group, from Li *et al.* [27^{**}].)

Whereas neurons in primary auditory cortex (A1) of rats change responses after training in a 'sound-maze' [36], cortical organization in A1 of cats is largely unchanged by training of a frequency discrimination task [37].

Professional musicians are faster in responding to a tactile co-activation task than non-musicians [38], indicating higher plasticity in 'trained' subjects. Hebbian co-activation by transcranial magnetic cortical stimulation with tactile stimulation improves tactile discrimination ability [39], and tactile co-activation induces significant

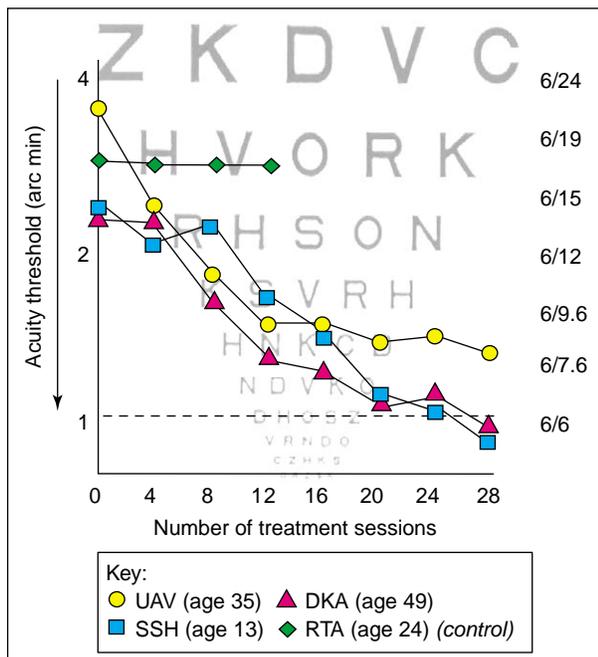
changes in somatosensory cortex (SI and SII) [40*,41*,42,43].

Olfactory learning might rely on changes in the odorant receptive fields of second and/or third order olfactory neurons of animals, hence again on a relatively peripheral level of processing, leading to the synthesis of experience-dependent receptive fields as a result of PL [44,45].

Consolidation of learning and visual rehabilitation of patients

New experimental data have broadened the evidence that consolidation of improvement achieved through PL requires sleep [46–49]. Both sleep and restful waking facilitate auditory tone learning [47]. Auditory training with a small number of words improves performance with these words and generalizes to novel words using the same phonemes but with different acoustic patterns. Sleep consolidates improvement in a spoken-language task [48] and the automaticity in an auditory discrimination task [49]. Training identification of vowels also improves performance and enhances amplitude of evoked potentials, decreasing their latency [50]. Finally, patients wearing a cochlear implant learn to partially adjust to changes in frequency-to-electrode assignment [51]. Unilateral lesions in macaques, conversely, severely disrupt learning and performance in a visual match-to-sample task [52*].

Figure 2



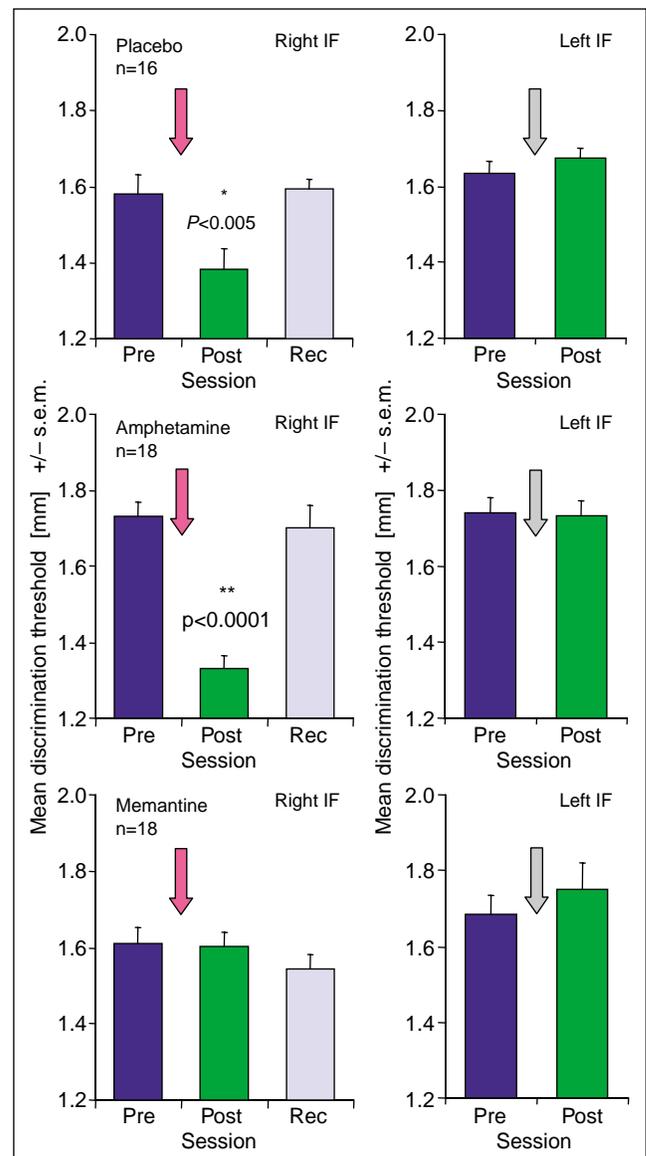
Improvement of visual acuity in three amblyopic patients as a function of training versus one control subject. All three patients substantially improve their visual acuity during the training period, whereas the control does not. (Used with permission from The National Academy of Sciences of the US, from Polat *et al.* [53**].)

Amblyopes (see glossary) are clearly benefiting from PL. Training improves contrast sensitivity of amblyopic eyes by about a factor of two (Figure 2; [53**]), and increases their acuity significantly [53**,54,55].

Neuronal mechanisms of perceptual learning: models and pharmacology

The steadily increasing amount of data and number of insights in PL enables the formulation of ever-improving models of PL, incorporating both specificity and

Figure 3



Mean somatosensory discrimination thresholds in humans improve significantly from before ('pre') to after ('post') training, at least under placebo and for the right index finger (IF) used for co-activation. Amphetamine increases the improvement for the trained side only while memantine prevents any change. No effects were found after a 24h interval ('rec'). (Used with permission from Science, from Dinse *et al.* [61**].)

generalization of learning [56–59]. Important features of these models are the implementation of recurrent (feed-back) connections [56,57], incorporating internal and external noise [57], and assessing the change of internal templates [58,59]. The models show that first, the reported sharpening of orientation tuning curves can account for the psychophysical data [56], second, PL seems to improve elimination of external noise, and third, it does this by retuning the internal templates [58,59].

The neuronal networks modified by PL are influenced by pharmacological agents [60,61,62], and by transcranial magnetic stimulation [63]. For example, improvement by co-activation in tactile two-point discrimination is eliminated by lorazepam, a γ -aminobutyric acid (GABA) receptor agonist [60], and by memantine, which blocks *N*-methyl-D-aspartate (NMDA) receptors [61]. Amphetamine, however, increases the improvement observed with PL (Figure 3; [61]). Acetylcholine seems to play a crucial role in plasticity of the olfactory system and to modulate olfactory PL [62].

Conclusions

Perceptual learning is often highly specific for rather low-level features of stimuli, such as their orientation. To achieve optimal performance, especially for this type of feature, irrelevant signals and noise have to be eliminated as early as possible during processing. To prevent interference of learning one task with performance in other tasks, the changes achieved on early levels have to be activated, in a task-dependent way, by top-down signals. Easier tasks do not have to involve the early processing levels, and hence improvement generalizes.

Given the task-dependence of some of the neuronal changes, it is difficult to find the exact neuronal correlates of PL using electrophysiology. Still, several positive reports are available, even on the single-cell level. Finally, the role of different neurotransmitters in PL is slowly emerging, along with applications created to help rehabilitation training in patients. Research in recent years has shown that perceptual learning improves performance in nearly all tasks investigated so far, and that features of vastly differing complexity can be learnt, ranging from straightforward contrast discrimination to detecting complex patterns such as x-rays of bombs hidden in suitcases. The underlying changes of the central nervous system can involve even early sensory cortices. It will be important to further clarify the neuronal mechanisms underlying perceptual learning — including the influence of drugs — and to try to use the resulting knowledge for the rehabilitation of patients suffering from sensory deficits, especially in the case of stroke patients.

Acknowledgements

M Fahle is supported by the German Research Council.

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