



Preface

Perceptual learning – The past, present and future



1. What is perceptual learning?

Perceptual learning is a long-term enhancement of a perceptual ability arising from perceptual experience (Lu et al., 2011; Sasaki, Nanez, & Watanabe, 2010). It may be viewed as a manifestation of perceptual and brain plasticity, especially in adults who have undergone a critical period of perceptual development in their early years. Research on perceptual learning is important not only for clarifying the mechanisms of perceptual plasticity but also for improving and restoring declining or damaged perceptual function resulting from disease or age (Andersen, 2012; Levi, 2012).

2. The third perceptual learning workshop in Nara, Japan

The Third International Perceptual Learning Workshop was held in Nara, Japan, 4–8 December, 2012. The workshop was organized by Mitsuo Kawato (Japan), Zhong-Lin Lu (USA), Dov Sagi (Israel), Yuka Sasaki (USA), Takeo Watanabe (USA), and Cong Yu (China). Leading researchers in perceptual learning from visual, auditory, and tactile psychophysics, cognitive neuroscience, monkey physiology, and computational neuroscience attended and gave presentations in the workshop. As in the First and Second International Perceptual Learning Workshops held, respectively, in Beijing, China, in 2009 and Eilat, Israel, in 2011, the presentations and discussions took place in a congenial and constructive environment, in the center of an old capital founded in 710 AD. Since the First Workshop, perceptual learning has become progressively more popular, with the number of published articles in the field increasing from around 100 in 2009 to about 150 in 2013. The scientific program of the Third Workshop included 28 talks:

- **Krystal R. Huxlin, Anasuya Das, Duje Tadin and Marisa Carrasco** “Properties of visual relearning in cortically blind fields – early insights into mechanisms of learning without an intact V1”.
- **Dov Sagi** “Perceptual learning and sensory adaptation: Close encounter”.
- **Karen Banai** “Learning following brief and intensive training: The case of time compressed speech”.
- **Sygal Amitay, Yu Xuan Zhang, Pete R. Jones and David R. Moore** “Perceptual learning: Top to bottom”.
- **Yin Yan, Minggui Chen, Malte Rasch, Si Wu and Wu Li** “Learning enhances coding efficiency in monkey V1”.
- **Marisa Carrasco, Martin Rolfs and Nick Murray-Smith** “Perceptual learning transfers to the location of predictive remapping”.
- **Uri Polat, Maria Lev, Oren Yehezkel, Moshe Fried, Ravid Doron and Anna Sterkin** “When perceptual learning can be generalized”.
- **Benjamin Thompson, Bosco S. Tjan and Zili Liu** “Perceptual learning of motion direction discrimination with suppressed and unsuppressed MT in humans: An fMRI study”.
- **Stephen A. Engel, Min Bao and Juraj Mesik** “Multiple temporally tuned mechanisms of visual adaptation”.
- **Barbara Doshier and Zhong-Lin Lu** “Perceptual learning: Interference and generalization”.
- **Ehud Zohary** “Fingerprints of learned object recognition seen in the fMRI activation patterns of lateral occipital complex”.
- **Hubert R. Dinse** “Tactile perceptual learning – role of mental states”.
- **Rufin Vogels and Hamed Zivari Adab** “Coarse orientation discrimination affects single unit response properties in early and late extrastriate areas”.
- **Zhong-Lin Lu** “Perceptual learning in adults with amblyopia”.
- **Kazuhiisa Shibata, Yuka Sasaki, Mitsuo Kawato and Takeo Watanabe** “Two stage model of perceptual learning revealed by fMRI”.
- **Takeo Watanabe, Kazuhisa Shibata and Yuka Sasaki** “Perceptual learning consists of reinforcement-driven exposure-based learning plus task-driven rule-based learning”.
- **Shaul Hochstein** “Programs of the brain”.
- **Miguel Eckstein and Matthew F. Peterson** “Learning optimal eye movements for face recognition tasks”.
- **Yuka Sasaki, Dongho Kim, Dongwha Kang, LiHung Chang and Takeo Watanabe** “Global connectivity changes between the visual cortex and higher-level cortical regions in association with perceptual learning revealed by diffusion tensor tractography and functional connectivity”.
- **Geoffrey Ghose and Katherine Weiner** “Sparse encoding and decoding is maintained in area V4 during shape learning”.
- **Beverly A. Wright and David F. Wright** “Little differences in the representations engaged during the acquisition and consolidation of auditory perceptual learning”.
- **Ben S. Webb** “Brain states and perceptual learning”.
- **Cong Yu, Wu Li and Yan Song** “Understanding perceptual learning and its specificity and transfer: Psychophysical and ERP evidence”.
- **Aaron Seitz** “Two stories of fast implicit learning”.
- **Merav Ahissar, Michael Herzog, Hilla Jacoby, Itay Lieder, and Ofri Raviv** “Can we enhance cognitive abilities by short intensive training?”.
- **Michael H. Herzog, Lukasz Grzeczowski, Aaron Clarke, Fred Mast and Merav Ahissar** “Interference in imagery perceptual learning”.
- **Jun Yun Zhang, Cong Yu, Stanley A. Klein and Dennis M. Levi** “Perceptual learning in amblyopic vision is cognitive learning”.
- **Mitsuo Kawato** “Decoded neurofeedback and BMI therapy”.

3. Articles in this special issue

There are twenty papers in this Third Special Issue on Perceptual Learning. Table 1 shows the main topics, which reveal an interesting diversification. While about half of the papers deal with conventional topics of perceptual learning, such as specificity and transfer of the trained feature, stages of perceptual learning, learning of primitive sensory features including orientation, motion, and luminance, task-irrelevant and exposure-based learning, noise reduction, feedback, task-difficulty and roving, by contrast the remaining papers discuss rather broader topics. Some of these papers deal with learning of complex features including objects and faces that, unlike primitive sensory features, may be processed at higher stages of visual processing. Other papers are concerned with learning to improve attention and the effects of aging on perceptual learning. Although studies of the roles of sleep and video games in perceptual learning have relatively long research histories, they have recently attracted much greater attention from researchers in other areas. These developments point to the growing maturity of the field, with traditional aspects of perceptual learning becoming better understood and its significance for interdisciplinary and other fields now more widely recognized.

The following is a summary of some of the key findings from individual papers.

The subject of the first paper is task irrelevant perceptual learning (TIPL) (Watanabe, Nanez, & Sasaki, 2001). In a typical TIPL experiment observers continuously monitor letters presented at fixation (main task; RSVP) while presented with additional surrounding task-irrelevant stimuli. Here, Lecrecq, Le Dantec, and Seitz present task irrelevant natural and urban scenes, finding that their later tested memory is enhanced when paired with a target letter as compared with a distractor letter in the trained RSVP task (Leclercq, Le Dantec, & Seitz, 2014). This surprising result suggests that the encoding of task-relevant targets is accompanied by a global memory event that captures episodic information.

Gao and Wilson (2014) reported that to discriminate a group of synthetic faces, observers implicitly learn the most significant geometric variations in addition to the prototype. Compared to actually seen faces, the observers more frequently recognized by mistake unseen faces that represent the first two principal components [eigenfaces (Turk & Pentland, 1991)] of the studied faces.

Table 1

The numbers of conventional and broader topics. More than one topic was selected from each of some papers.

| | |
|-----------------------------------|----|
| <i>Conventional topics</i> | |
| Task-irrelevant/implicit/exposure | 4 |
| Noise/reweight | 3 |
| Feedback | 2 |
| Specificity/transfer | 2 |
| Stage | 2 |
| Clinical | 1 |
| Roving | 1 |
| Task-difficulty | 1 |
| Total | 16 |
| <i>Broader topics</i> | |
| Sleep | 4 |
| Memory | 3 |
| Faces | 3 |
| Object | 1 |
| Learning of attention | 1 |
| Category | 1 |
| Video game | 1 |
| Aging | 1 |
| Eye movements | 1 |
| Total | 16 |

These results indicate that the types of summary statistics that the visual system can implicitly extract also include several principal components (Gao & Wilson, 2014).

Gold et al. (2014) demonstrated that human observers can incidentally learn a fixed sequence of 1D or 2D contrast noise that is repeated in multiple trials, but at a speed much slower than that with auditory noise. Reverse correlation indicates that contrasts occupying particular temporal positions that correspond to the mid and end points of a sequence had disproportionately heavy weight in observers' judgments. However, the observers cannot learn repeated temporally mirror symmetric noise sequences.

DeLoss, Watanabe, and Andersen (2014) examined perceptual learning of orientation discrimination in older adults. Their results showed that the degree of learning and transfer was related to task difficulty and the presence of external noise. For example, training with a difficult condition produced greater learning in the absence of external noise. In addition, improved orientation discrimination was not associated with the change of retinal luminance.

In this modeling study Liu, Doshier, and Lu (2014) extended their reweight model to account for the complex effects of feedback on perceptual learning (Herzog & Fahle, 1999; Liu, Lu, & Doshier, 2010; Seitz et al., 2006). They incorporated three major factors that facilitate perceptual learning: the external trial-by-trial feedback, the self-generated output as an internal feedback when no external feedback is available, and the adaptive criterion control based on the block feedback.

The efficiency of perception depends to a large degree on the way the eyes are moved across a visual scene. Peterson and Eckstein (2014) present a novel paradigm related to the role of eye-movements in perceptual learning, using face stimuli and the method of the ideal observer. In their face recognition task, learning varied across observers with changes in eye-movements explaining much of this variability. Importantly, improving image sampling by adopting better fixation patterns can almost double observers' efficiency. Thus it is of necessity to consider the mutual interactions between eye-movements and perceptual learning.

Amitay et al. (2014) review a possible modality-general mechanism of perceptual learning, through their own auditory perceptual learning work and others. Since *Vision Research* readers may not be familiar with the auditory perceptual learning literature, this may be a good opportunity to take a peek at work in a different sensory modality. Amitay et al. suggest that auditory perceptual learning is a conglomeration of sensory and non-sensory effects, and that internal noise and decision inefficiency limit the accuracy of perceptual decisions.

It has been suggested that perceptual learning is a strong tool to improve or restore vision of patients with amblyopia (Levi, 2012). An interesting question is whether perceptual learning can work as a remedy to deficits in more cognitive functions. Gori and Facoetti (2014) offer a review from the perspective that a major cause of dyslexia is the basic cross-modal letter-to-speech sound-integration deficit that might arise from a mild atypical development of the magnocellular-dorsal pathway. The proposal is to use perceptual learning as a strong tool to improve the impaired visual functions characterizing dyslexia and the visual deficits that could be developmentally related to an early magnocellular-dorsal pathway and selective attention dysfunction.

In a roving procedure, a task with either two different baseline conditions (e.g., incremental thresholds at 10 cd/m² and 40 cd/m²) or different magnitudes of discrimination (e.g., a 30 arcmin and a 20 arcmin wide bisection stimulus) are randomly interleaved from trial to trial. Many studies have shown that roving impairs both perceptual learning and task sensitivity (Adini et al., 2004; Kuai et al., 2005). Clarke et al. (2014) investigated the relationship between training and sensitivity in roving using a bisection task. They found that roving had no effect on sensitivity before training,

but impaired sensitivity after training. These results may provide some very strong constraints on algorithms of perceptual learning.

Many studies have shown that perceptual learning of motion direction is specific to the trained direction (Ball & Sekuler, 1987; Liu & Weinshall, 2000). Zhang and Yang (2014) show that perceptual learning of motion direction transferred to an opposite direction following the training-plus-exposure (TPE) procedure, in which participants were exposed to the opposite motion direction as irrelevant during a dot-number discrimination task. Such transfer occurred with TPE that was either simultaneous with or after motion direction training, but not with TPE before motion direction training. The TPE procedure and associated results present new theoretical challenges in understanding perceptual learning.

Goldhacker et al. (2014) examined the effects of informative feedback during training on perceptual learning of coherent motion and brain activity measured in fMRI in a highly systematic way. They found that informative feedback facilitates performance and, to a lesser extent, brain activity, especially for medium-to-high motion coherence levels. Surprisingly, feedback with lower motion coherences showed aversive effects on perceptual learning. They suggested interactions between feedback signals and internal reinforcement signals led to the results.

While much of current research in perceptual learning makes use of simple, often unidimensional, stimuli and tasks, perceptual skills depend on the ability to extract image features allowing for efficient object classification. Mettler and Kellman (2014) extend perceptual learning to a real-world like situation involving perceptual categories. They examined how learning can be optimized in complex tasks and whether learning procedures found to be efficient in other domains, such as memory, are effective in category learning. Using a butterfly classification task, they find that an adaptive, response-time based, category sequencing algorithm implementing laws of spacing derived from memory research enhances perceptual category learning and transfer to novel cases.

Learning of temporal structures have been linked to statistical or incidental types of learning. Baker et al. (2014) tested whether exposure to temporal sequences in a scene facilitates the visual recognition of upcoming stimuli. They found that exposure to structured without feedback improved following performance, whereas such performance enhancement was not observed after exposure to random structures. This effect transferred to untrained stimulus features. These results indicate that subjects acquired knowledge of the sequence structure.

Deveau, Lovcik, and Seitz (2014) took an integrative approach to perceptual learning. Instead of attempting to achieve perceptual improvements on a single task, they explored effects of learning of a set of component tasks that have individually contributed to increasing the speed, magnitude and generality of learning in a perceptual learning video game. They found broad-based benefits of video game training in a healthy adult population, including improvements in visual acuity, the full contrast sensitivity function, peripheral acuity, and contrast thresholds. These results have important implications for the design of visual rehabilitation therapies.

Attentional blink (AB) is a phenomenon observed in rapid serial visual presentation (RSVP) that is thought to reflect the capacity limitation of visual temporal attention (Chun & Potter, 1995; Raymond, Shapiro, & Arnell, 1992). When presented with a sequence of visual stimuli in rapid succession at the same spatial location on a screen, a participant will often fail to detect a second salient target (T2) occurring in succession if it is presented between 180 and 450 ms after the first one (T1). Choi and Watanabe (2012) showed that AB can be attenuated after a short period of the color-salient training, in which the second target (T2) within the AB period is given a salient color. In a paper published in this special issue, Choi and Watanabe (2014) examined

effects of color-salient training on repetition blindness (RB), a phenomenon also observed in RSVP in which participants often miss a target if it is identical to its preceding item. They found that color-salient training with a non-repeated T2 eliminated AB but did not remove RB, but color-salient training with a repeated T2 significantly reduced both AB and RB. The results suggest that color-salient training could increase the capacity of visual temporal attention.

Perceptual learning is known to improve stimulus discriminability, but does it modify stimulus appearance? An impressive series of demonstrations by the Backus group has indicated that the answer is positive (Haijiang et al., 2006). Using ambiguous stimuli (rotating Necker cube), Harrison and Backus (2014) found that perceptual biases induced by unambiguous cues were detected four weeks later. This result implies that the association between the different perceptual cues recruited by the perceptual system during the initial presentation (i.e. occlusion and disparity) remains intact until re-learned. Surprisingly, this persisting association is specific to retinal location, as most perceptual learning effects are.

The last four papers concern themselves with sleep and perceptual learning. Sleep was found to play an important role in the stabilization and consolidation of perceptual learning, but the function of sleep and the underlying relevant mechanisms are not clear, with current research suggesting multiple mechanisms (Sagi, 2011). Sasaki et al. have two papers related to sleep. In one paper, Tamaki et al. (2014) examined whether the first night effect, whereby subjects have difficulties to initiate and maintain good sleep in a novel experimental setting, affects spontaneous activation in the occipital cortex. They found that the first night diminishes power of slow wave activity in the early visual cortex especially in the first hour of sleep, indicating the importance of 'sleep adaptation'. That is, subjects cannot sleep well in the first night of an experiment, the sleep data may need to be collected after subjects are accustomed to sleep in the experimental setting. This procedure will be important to assess sleep effects on learning and memory. In the other paper, Bang et al. (2014) tested whether delta and sigma oscillations originated in the early visual cortex are involved in visual perceptual learning. They found that the power of sigma, not delta, oscillation is increased after learning, in high correlation with performance improvement. The finding suggests that sigma oscillations in the early visual cortex are involved in consolidation of visual perceptual learning.

McDevitt et al. (2014) studied differences between men and women in offline consolidation of perceptual learning of motion direction discrimination. They found that rapid eye movement (REM) sleep facilitates learning consolidation, but that male observers showed high specificity of learning to the trained motion direction, whereas female observers showed broad learning transfer to other untrained directions. Male observers also tended to have a greater learning effect at the trained direction.

Baeck et al. (2014) studied the effect of sleep on perceptual learning on complex objects. While recognition of objects improves with training, task performance improves between sessions without further training as well. Although studies that showed effects of sleep on perceptual learning used primitive visual features, Baeck has shown that perceptual learning with complex objects also obtains benefit from post-training sleep.

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