



## Review

## Neuronal mechanisms of visual perceptual learning



Hironori Kumano, Takanori Uka\*

Department of Neurophysiology, Graduate School of Medicine, Juntendo University, 2-1-1 Hongo, Bunkyo, Tokyo 113-8421, Japan

## HIGHLIGHTS

- Where and how do long-term plastic changes underlying perceptual learning occur?
- Neurophysiological research using non-human primates is reviewed.
- Results are discussed in the context of learning specificity.
- Possible mechanisms that support learning-related plasticity are discussed.

## ARTICLE INFO

## Article history:

Received 3 April 2013

Accepted 19 April 2013

Available online 29 April 2013

## Keywords:

Macaque monkey

Visual cortex

Neurophysiology

Reinforcement learning

## ABSTRACT

Numerous psychophysical studies have described perceptual learning as long-lasting improvements in perceptual discrimination and detection capabilities following practice. Where and how long-term plastic changes occur in the brain is central to understanding the neural basis of perceptual learning. Here, neurophysiological research using non-human primates is reviewed to address the neural mechanisms underlying visual perceptual learning. Previous studies have shown that training either has no effect on or only weakly alters the sensitivity of neurons in early visual areas, but more recent evidence indicates that training can cause long-term changes in how sensory signals are read out in the later stages of decision making. These results are discussed in the context of learning specificity, which has been crucial in interpreting the mechanisms underlying perceptual learning. The possible mechanisms that support learning-related plasticity are also discussed.

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## Contents

1. Introduction.....	75
2. Neurophysiology of perceptual learning in the visual cortex.....	76
3. Changes in the read-out of sensory neurons during learning.....	76
4. Transfer of perceptual learning.....	77
5. Hypothetical mechanisms underlying plastic changes during learning.....	78
6. Conclusion.....	79
References.....	79

## 1. Introduction

Psychophysical sensitivity during the performance of sensory discrimination or detection tasks can improve with training, even in adults well beyond critical developmental periods. This is known as perceptual learning [17,18,21]. Improvements in performance

range from simple sensory discriminations (e.g., discrimination of line orientation) to complex identifications (e.g., identifying tumors in x-rays) and often last for several years [27]. This suggests that long-term plastic changes occur within the adult brain. Where and how plastic changes occur is one of the most frequently asked question in systems neuroscience, particularly regarding vision [30,57]. Here, neurophysiological studies that examined the neural mechanisms underlying this type of perceptual learning in non-human primates are reviewed. Due to space limitations, important issues, such as human perceptual learning and the effects of attention, will not be covered, and readers can refer to recent reviews on these topics [43,46].

\* Corresponding author.

E-mail address: [uka@juntendo.ac.jp](mailto:uka@juntendo.ac.jp) (T. Uka).

Many psychophysical studies using visual perception tasks have found that learning effects are often, but not always, specific to the stimulus configuration used during training (e.g., the orientation or retinotopic location of the visual stimulus) [15,19,26,38,47]. Because of this specificity, researchers have suggested that plastic changes underlying perceptual learning occur within the primary visual cortex (V1), where neurons have small receptive fields (RFs) and are selective for simple stimulus features such as orientation. Indeed, for auditory or somatosensory perceptual learning, substantial changes, including topographic reorganization, enlargement of RFs, and sharpening of stimulus selectivity, occur within the primary sensory areas of monkeys [25,41,42]. These physiological findings further raise the possibility that plastic changes in V1 may underlie visual perceptual learning.

## 2. Neurophysiology of perceptual learning in the visual cortex

Several studies have examined the hypothesis that long-term plastic changes occur in V1 during training and that these changes are the neural basis of perceptual learning. In two of these studies, monkeys were trained on a fine orientation discrimination task around a fixed orientation at a fixed location [16,48]. Behavioral data from both studies show some degree of location or orientation specificity in performance improvement. After training, the authors recorded from V1 and compared response properties of neurons with RFs that overlap the trained location with those of neurons in the opposite hemisphere. Neither topographic changes nor increases in the number of neurons selective for the trained orientation were observed in either study. Schoups et al. [48] found a slight increase in sensitivity to fine orientation difference, quantified as the slope of orientation-tuning curves, in the trained hemisphere. Ghose et al. [16] reported no such change. Similarly, no change in neuronal characteristics were found using a three-line bisection task in which monkeys judged whether a center line was closer to one of two flanking reference lines [10]. Together, these data suggest little or no change in the sensitivity of single neurons in V1 and indicates that correlates of perceptual learning may be found in higher visual areas.

Subsequent studies examined area V4, a region along the ventral visual pathway associated with a later stage of cortical visual processing, using the same fine orientation discrimination task [40,59]. These studies reported larger changes in response properties in V4 than in those in V1, including an increase in response strength, a decrease in response variability, and an increase in the slope of orientation-tuning curves around the trained orientation. These changes, however, were an order of magnitude smaller than were the changes in performance observed behaviorally [40]. Thus, it remains unclear whether the modest changes in the response characteristics of V4 neurons could account for the observed degree of perceptual learning.

These physiological studies examined neuronal responses only after the training of a task was complete and compared neuronal characteristics in the trained hemisphere with those in the opposite, untrained hemisphere as an internal control. This experimental strategy may underestimate possible effects of training on neuronal characteristics. Specifically, behavioral data from these studies suggest that learning was not completely specific to the trained location, and some degree of transfer was observed (see Section 4). Thus, if perceptual learning transferred across locations, training at a fixed location in the test hemifield could cause plastic changes in the “control” hemisphere, leading to an underestimation of the effects of training. One way to overcome this difficulty is to examine neuronal activities throughout the course of training and compare the neuronal characteristics of early and late stages

of training. Using this strategy in monkeys trained to discriminate orthogonal orientations masked by noise, Adab and Vogels [1] found substantial increases in the sensitivity of V4 neurons that were comparable to behavioral improvements. Although this finding points to the importance of examining neurons throughout the course of training, the mixed results concerning V4 may be attributable to the different kinds of task that were used (i.e., fine vs. coarse orientation discrimination) across studies.

If long-term plastic changes in sensory areas underlie perceptual learning, these changes should occur within an area that plays a prominent role in that task. Thus, ideally, an experiment should use a framework in which the relationship between neuronal activities and perceptual performance is firmly established [36]. In this regard, the middle temporal (MT) visual area, a region along the dorsal visual pathway associated with a later stage of cortical visual processing, is a good candidate for examining the neural mechanisms of perceptual learning. Neurons in MT have been consistently shown to contribute to motion-direction discrimination [5,6,33,45] and binocular depth discrimination [8,11,53–55]. Law and Gold [28] examined the activity of single neurons in the MT and the lateral intraparietal (LIP) areas during training on a motion-direction discrimination task. They did not observe changes in the motion-direction sensitivity of MT neurons during the course of training. Similarly, a recent study from our lab [56] did not find any improvement in the sensitivity of MT neurons to binocular depth during long-term training. Thus, neuronal characteristics in V1 and MT seldom change with training, whereas those in V4 can change depending on the experiment. Possible reasons for this difference between V1-MT and V4 will be discussed later in Section 5.

## 3. Changes in the read-out of sensory neurons during learning

Given that there is little or no change in sensitivity occurring in neurons in early or mid-level visual areas, alternative mechanisms should be at work during long-term improvement in performance. Several psychophysical and modeling studies have proposed that perceptual learning can be explained by an adjustment of weights through which basic sensory channels affect decision making [12,32,37]. Thus, perceptual learning can occur via improvements in how sensory signals are decoded or read out by decision-making mechanisms. This type of model can also account for the location specificity of perceptual learning because training strengthens sensory channels that are relevant to the task, including spatial location [13].

The aforementioned study by Law and Gold [28] supports this hypothesis. In the context of the motion-direction discrimination task, the responses of LIP neurons represent decision formation by integrating sensory signals from motion-sensitive areas such as MT [44,51]. Law and Gold [28] found that LIP responses substantially change with training. Early in training, LIP responses depend only on the monkey's subsequent choice and not on the strength of motion stimuli. With extended training, LIP responses gradually become dependent on motion strength, and the rate of build-up activity increases during training. These characteristics of LIP neurons are consistent with an increasingly selective read-out from sensitive MT neurons.

Along with changes in the neuronal responses of a higher-order decision area, the read-out of sensory neurons can be inferred from the relationship between responses of sensory neurons and the animal's choices; this is often referred to as choice probability (CP; [6]). CP represents the probability that one could predict the monkey's choices from its neuronal responses. For many perceptual discrimination tasks, the CPs of sensory neurons have been shown to be significantly higher than chance [6,34,39,54],

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