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Is perceptual learning associated with changes in a sensory region?

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Abstract

Perceptual learning is defined as long-term improvement in perceptual abilities as a result of perceptual experiences. It is controversial as to whether perceptual learning is associated with changes in a sensory region of the brain or not. Here, we review research that supports, or otherwise, the sensory change hypothesis and discuss what needs to be done in the future to answer this question more definitively.

Introduction

Recently, perceptual learning (the long-term improvement in perceptual abilities, including distinguishing differences in sensory features, such as contrast and orientation, as a result of repeated perceptual experiences) has attracted much attention on the part of vision scientists, with the hope that research on perceptual learning will lead to a better understanding of the mechanism of perceptual plasticity. However, it is highly controversial as to what part of the brain is associated with perceptual learning. Here, we will discuss the controversy.

Specificity of perceptual learning

It has been suggested that perceptual learning is unique and distinguishable from other forms of learning in many aspects, including task rules, associations, and strategies. One of the unique characteristics of perceptual learning is that perceptual improvements are often specific to trained stimuli. In one study, for example, after presentation of three parallel lines, including one center task line and two lateral reference lines, participants were asked to indicate whether the center line appeared closer to the left or the right reference line. After several weeks of training, participants improved their performance drastically. However, this improvement was not found when participants were tested with novel orientations and novel target positions [1]. Such specificity has been found in various features, including orientation (and its vicinity) [2-4], motion direction of training stimuli [5,6], and also retinotopic location where the stimuli are presented [2,4].

This specificity is consistent with the characteristics of neurons in areas early in the sensory visual pathway with small receptive fields and specific responses to primitive stimulus features [7,8]. Thus, the specificity suggests sensory changes are associated with perceptual learning.

A number of studies, however, have indicated that such high specificity is not always shown in perceptual learning. One such study showed that the extent of the transfer of performance improvement from the trained to untrained orientations may depend on the degree of task difficulty [9]. A more recent study developed a novel double-training paradigm that employed conventional feature training (e.g. contrast) at one retinal location and additional training with an irrelevant feature/task (e.g. orientation) at a second retinal location, either simultaneously or at a different time. This approach allowed perceptual learning of a task to transfer to a new retinal location [10].

Although several studies (including the above experiments) have reported a few exceptions to the specificity of perceptual learning, the specificity is still considered as one of the main properties of perceptual learning.

Changes in brain areas associated with perceptual learning

The most straightforward way to test whether changes of sensory areas occur after perceptual learning is to look directly inside the brain, and various studies have tried to figure out which regions are altered as a result of perceptual learning.

A number of these studies have focused on changes in the primary visual cortex (V1), the earliest cortical stage of the visual area, because neurons of V1 have the smallest receptive field and respond highly selectively to specific features, including orientation and location: such characteristics of V1 neuron activity are consistent with aspects of specificity in perceptual learning [8]. Studies have found enhanced tuning specificity of neurons in V1 in monkeys [11] and cats [12] or increased blood-oxygen-level-dependent (BOLD) signals in the trained area of V1 in humans [13-16].

However, some single-unit studies (i.e. recording the electrical impulses in single neurons) of monkeys have failed to find any changes in V1 after perceptual learning. One study showed that extensive training with monkeys did not change the selectivity and responsiveness of neurons in V1 [17]. Another study reported that the basic properties of receptive fields of V1 neurons, such as location, size, and orientation selectivity, were not changed after perceptual training, although the influence of contextual stimuli (that were placed outside the receptive fields) on the activity of V1 neurons was altered [18].

Other studies have focused on changes in higher sensory regions. Yang and Maunsell [19] found that perceptual learning induced changes not in V1 but in V4 in monkeys. It has also been found that neurons in the middle temporal complex (MT) region of the visual cortex in monkeys were better tuned to the trained motion direction, at least during the experiment [20].

On the other hand, some recent studies using monkeys have suggested that perceptual learning is associated with changes outside the sensory regions altogether [21,22]. It has been found that, while perceptual learning of coherent (group) motion was not associated with responses in neurons in the MT area, it was in the lateral intraparietal area, which is usually regarded as being beyond the sensory system, and is related to perceptual decision-making [22]. This finding is consistent with a well-established model, in which perceptual learning results from changes in weights of connections between the sensory areas and the decision-making areas [23].

Conclusion

Controversies remain regarding whether or not perceptual learning is associated with changes in the sensory region of the brain. One of the main difficulties in addressing and answering this question lies in the fact that different experiments of perceptual learning have been conducted with different sets of stimuli, methods, and paradigms, without the perspective of systematically investigating perceptual learning. These discordances of experimental conditions have given rise to different findings. Thus, in order to resolve the controversy, standardizing experimental conditions in which perceptual learning occurs should be a priority.

Abbreviations

BOLD, blood-oxygen-level-dependent; MT, middle temporal complex; V1, primary visual cortex.

Competing interests

The authors declare that they have no competing interests.

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