Perceptual Learning: Cortical Changes When Cats Learn a New Trick

A new study has found that the tuning properties of neurons in the primary visual cortex of cats change as they learn an orientation-discrimination task, casting new light on the neuronal basis of perceptual learning.

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Performance on perceptual tasks improves with training. Sustained improvements that reflect better processing of incoming sensory information are called perceptual learning. Because perceptual learning is a robust phenomenon even in adults who have long passed the well-known early ‘critical period’ of cortical plasticity, understanding its neural basis should lead to a better understanding of neural plasticity in the adult brain [1]. In a recent report in *Current Biology*, Hua and colleagues [2] provide new insights into a possible role for plasticity at the level of the primary visual cortex in cats for a form of visual perceptual learning.

Visual information is processed in multiple stages, from the retina through subcortical and cortical visual areas to higher-order cortical areas that use the visual information to guide behavior. The issue of which brain area(s) undergoes the changes responsible for perceptual learning has been controversial. In one view, which we call the ‘V1 hypothesis’ [3], perceptual learning is associated with changes in the primary visual cortex (V1), the earliest cortical area onto which visual signals are projected. Psychophysical studies have shown that some forms of perceptual learning are highly specific for features of the training stimuli, such as their orientation, motion direction, contrast, location and even the eye-of-origin. Such high degrees of specificity are consistent with some of the properties of neurons in V1, so the V1 hypothesis assumes that perceptual learning is associated with changes in the sensory representation in V1.

There are, however, other hypotheses that posit that perceptual learning involves changes further along the visual processing pathway. For example, according to the read-out hypothesis [4,5], changes in V1 either do not occur or are not sufficient to yield better performance in a perceptual task. Instead, perceptual learning is associated with changes in connectivity between the sensory representation of the visual stimulus (possibly limited to the features experienced during training) and a higher decision-making unit.

Which hypothesis do neurophysiological studies support? The results of many functional magnetic resonance imaging (fMRI) studies with human subjects are in accord with the V1 hypothesis. In particular, fMRI signals in the region of V1 representing the trained location are changed in association with perceptual learning [6,7]. However, single unit-recording studies in monkeys have provided inconsistent results. For example, Schoups *et al.* [8] found that orientation tuning curves of monkey V1 neurons changed as a result of training on an orientation identification task. Using a similar — but not identical — method, Ghose *et al.* [9] found no evidence for changes in V1. Other single-unit studies found neural activity changes in area V4 of monkeys after training on an orientation-discrimination task [10], or in the lateral intraparietal area (LIP) after training on a motion direction-discrimination task [5], but neither study reported changes in V1.

In contrast to these previous studies in monkeys, Hua *et al.* [2] found substantial changes in V1 of cats in association with perceptual learning. The cats were trained on an orientation-discrimination task. Their ability to discriminate low-contrast stimuli improved with training, with the biggest improvements centered on the ranges of spatial frequencies used during training. These improvements in performance were accompanied by a refinement of the tuning properties of V1 neurons responding specifically to or around the spatial frequency of the trained orientation stimulus. The results provide compelling evidence for changes in V1 neurons in association with perceptual learning. What can and what cannot be inferred from the results? A number of questions and answers come to mind.

Might the differences between the various studies, mentioned above, be due to differences in what is measured by fMRI versus single-neuron recordings? BOLD signal measured by fMRI is thought to correlate more highly with field potentials in neuronal activity, which can be driven strongly by synaptic potentials, than with the action potentials measured by single-neuron recording [11]. Therefore, it is possible that fMRI activation in V1 primarily reflects not the spiking output of V1, but rather its input, which arises from both the ascending visual pathway and direct and indirect projections from higher cortical areas. Accordingly, fMRI activation in V1 [6,7,12] in association with perceptual learning might arise from changes in the higher-order structures that provide it with input. However, the results of Hua *et al.* [2] suggest that this explanation is at best incomplete, because they found changes in the output activity of V1 neurons.

Do different species have different mechanisms of perceptual learning? We do not yet know the answer to this question, but a survey of prior results suggests that this is a possibility. Evidence for learning-related changes in V1 come from studies of cats and humans, whereas most of the evidence against this hypothesis comes from studies with monkeys. Further studies are needed to clarify this issue.

Do different procedures lead to different types of neuronal changes? The answer is highly likely to be ‘yes’. To study perceptual learning, different groups often use experimental procedures that differ in at least one of the following four ways. First, there are three different types of single-task procedures used in perceptual learning studies: detection of (the presence of) a feature [13]; discrimination between features [3]; and mere exposure to a feature that is irrelevant to a given task [14]. Furthermore, some recent

Figure 1. The perceptual learning experiment of Hua *et al.* [2].

In training, a cat had to choose the one stimulus that contained the same orientation as the pre-determined orientation. Upon a 'correct' response, the luminance contrast of the presented stimuli decreased.

studies have involved training on two tasks, rather than just one [15]. It is hard to imagine that exactly the same neural circuit is recruited for these different task procedures.

Second, perceptual learning has been studied for tasks involving different visual features, including orientation, motion direction, color, contrast, spatial and temporal frequency and vernier acuity. These different features are processed in different ways and, at least in part, at different sites in the brain.

Third, even if the same basic task and feature are used, the procedures can vary. For example, the procedures for an orientation-identification task used by Hua *et al.* [2], Schoups *et al.* [8] and Ghose *et al.* [9] are substantially different. In the study by Hua *et al.* [2], a cat was presented with two large visual patches, each of which contained a different orientation (Figure 1). The task was to indicate which patch contained a pre-determined orientation. After a correct response, the contrast of the patches decreased for the next trial. In the study by Schoups *et al.* [8], a monkey was presented with a single patch that was much smaller than that used by Hua *et al.* [2]. The task was to judge whether the orientation of the patch was either clockwise or counterclockwise compared to a predetermined reference orientation. The key experimental variable was the angular difference between the presented and reference orientations, instead of stimulus contrast as in Hua *et al.* [2]. In the study by Ghose *et al.* [9], the monkeys were required to judge whether the orientations of two serially presented patches were identical.

Fourth, task difficulty varies across different studies. It has been suggested that different degrees of task difficulty, and possibly the associated differences in attentional demands, lead to changes in different cortical areas [16,17].

Thus, given the many different conditions that have been used in studies of perceptual learning, it is perhaps not so surprising that such different results have been obtained. Indeed, it seems likely that the neural locus of perceptual learning is not confined to a single site in the brain. Rather, it is important to continue to have studies like the work of Hua *et al.* [2] that carefully characterize the conditions that give rise to a particular form of plasticity, in V1 or beyond.

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