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Report

Perceptual Learning of Contrast Detection in the Human Lateral Geniculate Nucleus

Highlights

- Contrast learning shows specificity to the trained eye and visual hemifield
- Contrast learning boosts the activity of the M layers of the LGN
- Perceptual learning in human adults can occur as early as at the thalamic level

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In Brief

Yu et al. reveal that perceptual learning of contrast detection leads to an eye- and hemifield-specific neural response increase to low contrast in the M layers of the LGN and suggest that visual training can induce plasticity in subcortical nuclei.

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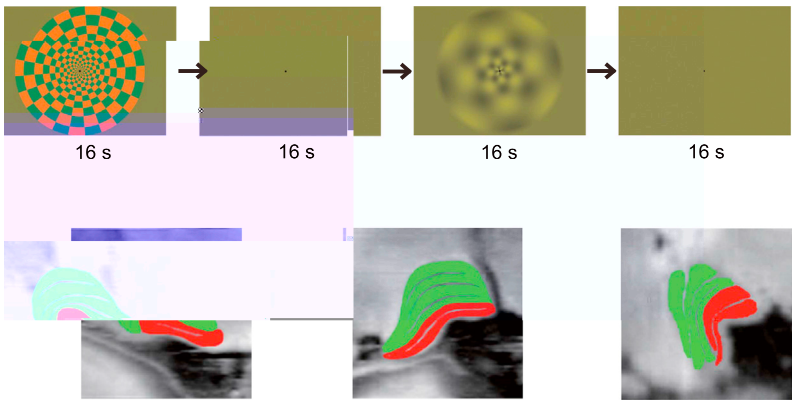
voxels was further constrained by the anatomical locations of the LGN based on high-resolution T1 images. On the T1 images in Figure 2A, which shows the LGN from a representative subject, the LGN appeared darker relative to surrounding brain tissues. The LGN is the thalamic component in the retinocortical projection and has been traditionally viewed as a passive relay station for retinal signals on their way to the primary visual cortex, or V1 [13]. This view has been challenged recently. There is growing evidence from human fMRI and monkey neurophysiology studies that neural responses in the LGN are influenced by perceptual and cognitive tasks (see [14] for a review).

Using the counterphase flickering checkerboard stimuli, we measured fMRI contrast response functions in the ROIs at three

Figure 2. FMRI
sagit tal, coronal, or axial views,
arrows. The second
the subject's LGN
(B) Counterphase



day × 100%) and the BOLD signal change at the 6% contrast level. The correlation was significant in the M layers ($r = 0.636$, $p < 0.05$), but not in the P layers ($r = -0.104$, $p = 0.712$), suggesting a fundamental role of the M layers in this learning (Figure 4B).

DISCUSSION

One month of training on a near-threshold contrast detection task led to a significant improvement in human subjects' contrast sensitivity, which was specific to the trained eye and the trained visual hemifield. Parallel to the behavioral learning effect, training also resulted in an eye- and hemifield-specific response increase to low contrast in the M layers of the LGN, but not in the P layers, V1, V2, or V3. Remarkably, the neural response enhancement in the M layers was closely associated with the contrast sensitivity improvement. Though it is traditionally believed that perceptual learning is underpinned by plasticity mechanisms at the cortical level, our findings demonstrate that, even at the thalamic level, neural circuits are not hardwired, and perceptual learning can modify receptive field properties of the LGN neurons.

It has been shown that perceptual learning can change cortical processing of trained stimuli in various ways, such as sharpening tuning curves [6, 12, 22], improving the stability of neural activation patterns [11, 23], enhancing neural response [24, 25], and re-

targets presented at the same retinal location to the untrained eye, which is in line with the eye specificity property of this kind of behavioral learning [5].

Is this LGN response enhancement a long-lasting change, and does it serve as a long-term mechanism of contrast detection learning? One recent study [35] measured the dynamics of subjects' behavioral performance with a texture detection task [5] and their V1 activation over a long time course of perceptual learning. Within the first few weeks of training, V1 activation in a subregion corresponding to the trained location and task performance both increased. However, while the improved performance was maintained 2 weeks after training, the V1 activation decreased to the level observed before training. Similar transient response enhancements were also found in the fusiform face areas immediately after training on a face discrimination task [11]. Both of the studies challenged the role of the transient response enhancements immediately after training in perceptual learning. In the present study, we did not measure brain signals after the post-training test to examine the persistence of the response enhancement to the low contrast. Nevertheless, the significant correlation between the behavioral and neural enhancements provides deterministic evidence for the crucial role of the M layers in the contrast detection learning, at least in the learning effect immediately after training.

Unlike previous studies [28–30], we did not observe training-induced response increase at the cortical level (i.e., V1). Here are several possible reasons. First, the fMRI measurement is not sensitive enough to detect such small changes (if there are any) that might be also specific to the trained eye and M neurons. In V1–V3, BOLD signals from individual voxels reflect mixed neural signals from left and right eye neurons and from M and P neurons, which could not be separated due to the limit of the current fMRI spatial resolution. Second, subjects were trained for the glutamate receptor agonist to block visual responses in on-center retinal ganglion cells and found that the inactivation led to a rapid emergence of off-center responses from on-center neurons in the LGN. A significant stride we made in the present study is that, without such abnormal visual experience (i.e., eyelid closure or pharmacological inactivation), even regular practice could profoundly change local receptive field properties of the LGN neurons in human adults. Recently, it has been recognized that the LGN and other thalamic structures actively regulate information transmission to the cortex and between cortical areas using various mechanisms, thereby contributing to perception and cognition much more than we previously believed [14, 41]. Exploring the functional plasticity of the subcortical structures induced by training is an important research topic in the future, which is necessary for us to fully understand the adaptive nature of perceptual and cognitive information processing in the brain.

EXPERIMENTAL PROCEDURES

The procedures and protocols used in this study were approved by the human subject review committee of Peking University. Complete procedures can be found in the Supplemental Information.

SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.09.034.

AUTHOR CONTRIBUTIONS

Q.Y. and F.F. designed the study. Q.Y. and J.Q. conducted the experiments. Q.Y., P.Z., and F.F. analyzed the data and wrote the manuscript.

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