Current Biology

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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SUMMARY

The brain is continuously modified by perceptual experience throughout life. Perceptual learning, which refers to the long-term performance improve-



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 contrast levels (6%, 24%, and 96%). During scanning, subjects performed a demanding task to detect the color change of the fixation point (Figure 2B). Therefore, the peripheral checkerboard stimuli were task irrelevant. The fMRI contrast response functions are shown in Figure 2C. For each ROI and each test condition, blood-oxygen-level dependent (BOLD) amplitudes were submitted to a repeated measures ANOVA, with training (preand post-training) and contrast (6%, 24%, and 96%) as withinsubject factors. The main effects of contrast were significant (LGN: all Fs(2, 38) > 82.82, p < 0.001; V1: all Fs(2, 38) > 142.77, p < 0.001; V2: all Fs(2, 38) > 168.93, p < 0.001; V3: all Fs(2, 38) > 122.98, p < 0.001, Bonferroni corrected). The BOLD responses increased with contrast. The main effects of training were not significant (LGN: all Fs(2, 19) < 3.195, p > 0.36; V1: all Fs(2, 19) < 0.378, p = 1; V2: all Fs(2, 19) < 0.445, p = 1; V3: all Fs(2, 19) < 1.217, p = 1). The interaction effect between training and contrast was only significant in the THTE condition in the LGN (THTE: F(2, 38) = 6.839, p < 0.05; UHTE: F(2, 38) = 0.567, p = 1; THUE: F(2, 38) = 0.350, p = 1; UHUE: F(2, 38) = 1.408, p = 1, Bonferroni corrected). Furthermore, post hoc t tests showed that the BOLD response after training was significantly

to lifferentially activate the M (M stimulus) and P (P stimulus) neurons in 15 of the 20 subjects. The P stimulus was a high-spatial-nequency isoluminant red/green squar wave parern and was counterphase flickered at 1 Hz. The M stimulur was a low-spatial-frequency sine wave pattern, with 30 b luminance contrast, and was counterphase flickered at 7.5 Hz (Figure 3A). The M layers of the LON were identified as loxels shoving a gleater response to the M stimulus than to Le P stimulus, and vice versa for the identification of the P layers. It should be noted that, due to the spatial resolution limit of fMRI, some vorels in the identified M or P layers might contain both M and P neurons (see [20], in which M layers and P layers are approximately 2 and 4 mm thick, respectively). However, it is safe to claim that voxels identified as located

20 s

20 s

°a:

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 traininginduced 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 oncenter 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 signibcant 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 Þeld 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 Þgures 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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REFERENCES

- 1. Sagi, D. (2011). Perceptual learning in vision research. Vision Res.51, 1552D1566
- 2. Watanabe, T., and Sasaki, Y. (2015). Perceptual learning: toward a comprehensive theory. Annu. Rev. Psychol. 66, 197D221.
- Buonomano, D.V., and Merzenich, M.M. (1998). Cortical plasticity: from synapses to maps. Annu. Rev. Neurosci. 21, 149D186
- Gilbert, C.D., Li, W., and Piech, V. (2009). Perceptual learning and adult cortical plasticity. J. Physiol. 587, 2743D2751.
- Karni, A., and Sagi, D. (1991). Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. Proc. Natl. Acad. Sci. USA 88, 4966D4970
- Schoups, A., Vogels, R., Qian, N., and Orban, G. (2001). Practising orientation identibcation improves orientation coding in V1 neurons. Nature 412, 549D553
- Law, C.-T., and Gold, J.I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. Nat. Neurosci. 11, 505D513

- Kahnt, T., Grueschow, M., Speck, O., and Haynes, J.-D. (2011). Perceptual learning and decision-making in human medial frontal cortex. Neuron 70, 549D559
- Dosher, B.A., Jeter, P., Liu, J., and Lu, Z.-L. (2013). An integrated reweighting theory of perceptual learning. Proc. Natl. Acad. Sci. USA 110, 13678D 13683.
- Yan, Y., Rasch, M.J., Chen, M., Xiang, X., Huang, M., Wu, S., and Li, W. (2014). Perceptual training continuously repres neuronal population codes in primary visual cortex. Nat. Neurosci. 17, 1380D1387.
- Bi, T., Chen, J., Zhou, T., He, Y., and Fang, F. (2014). Function and structure of human left fusiform cortex are closely associated with perceptual learning of faces. Curr. Biol. 24, 222D227.
- Chen, N., Bi, T., Zhou, T., Li, S., Liu, Z., and Fang, F. (2015). Sharpened cortical tuning and enhanced cortico-cortical communication contribute to the long-term neural mechanisms of visual motion perceptual learning. Neuroimage 115, 17Đ29
- Derrington, A. (2001). The lateral geniculate nucleus. Curr. Biol. 11, R635D R637.
- 14. Saalmann, Y.B., and Kastner, S. (2011). Cognitive and perceptual functions of the visual thalamus. Neuron 71, 209D223
- Cheng, K., Waggoner, R.A., and Tanaka, K. (2001). Human ocular dominance columns as revealed by high-Þeld functional magnetic resonance imaging. Neuron 32, 359Đ374
- Derrington, A.M., and Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. J. Physiol. 357, 219D240
- Hubel, D.H., and Wiesel, T.N. (1966). Effects of varying stimulus size and color on single lateral geniculate cells in Rhesus monkeys. Proc. Natl. Acad. Sci. USA 55, 1345D1346
- Zhang, P., Zhou, H., Wen, W., and He, S. (2015). Layer-specific response properties of the human lateral geniculate nucleus and superior colliculus. Neuroimage 111, 159D166
- Zhang, P., Wen, W., Sun, X., and He, S. (2016). Selective reduction of fMRI responses to transient achromatic stimuli in the magnocellular layers of the LGN and the superPcial layer of the SC of early glaucoma patients. Hum. Brain Mapp. 37, 558D569
- Andrews, T.J., Halpern, S.D., and Purves, D. (1997). Correlated size variations in human visual cortex, lateral geniculate nucleus, and optic tract. J. Neurosci. 17, 2859D2868
- Denison, R.N., Vu, A.T., Yacoub, E., Feinberg, D.A., and Silver, M.A. (2014). Functional mapping of the magnocellular and parvocellular subdivisions of human LGN. Neuroimage 102, 358D369
- 22. Yang, T., and Maunsell, J.H. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. J. Neurosci. 24, 1617Đ1626
- Adab, H.Z., and Vogels, R. (2011). Practicing coarse orientation discrimination improves orientation signals in macaque cortical area v4. Curr. Biol. 21, 1661D1666
- Zohary, E., Celebrini, S., Britten, K.H., and Newsome, W.T. (1994). Neuronal plasticity that underlies improvement in perceptual performance. Science 263, 1289D1292
- Schwartz, S., Maquet, P., and Frith, C. (2002). Neural correlates of perceptual learning: a functional MRI study of visual texture discrimination. Proc. Natl. Acad. Sci. USA 99, 17137Đ17142
- Chen, N., Cai, P., Zhou, T., Thompson, B., and Fang, F. (2016). Perceptual learning modiPes the functional specializations of visual cortical areas. Proc. Natl. Acad. Sci. USA 113, 5724D5729
- Ghose, G.M., Yang, T., and Maunsell, J.H. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. J. Neurophysiol. 87, 1867Đ 1888.
- Furmanski, C.S., Schluppeck, D., and Engel, S.A. (2004). Learning strengthens the response of primary visual cortex to simple patterns. Curr. Biol. 14, 573D578

- Bao, M., Yang, L., Rios, C., He, B., and Engel, S.A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. J. Neurosci. 30, 15080–15084.
- Hua, T., Bao, P., Huang, C.-B., Wang, Z., Xu, J., Zhou, Y., and Lu, Z.-L. (2010). Perceptual learning improves contrast sensitivity of V1 neurons in cats. Curr. Biol. 20, 887–894.
- Sowden, P.T., Rose, D., and Davies, I.R. (2002). Perceptual learning of luminance contrast detection: specific for spatial frequency and retinal location but not orientation. Vision Res. 42, 1249–1258.
- Blasdel, G.G., and Fitzpatrick, D. (1984). Physiological organization of layer 4 in macaque striate cortex. J. Neurosci. 4, 880–895.
- Rosa, M.G., Gattass, R., Fiorani, M., Jr., and Soares, J.G. (1992). Laminar, columnar and topographic aspects of ocular dominance in the primary visual cortex of Cebus monkeys. Exp. Brain Res. 88, 249–264.
- Hawken, M.J., and Parker, A.J. (1984). Contrast sensitivity and orientation selectivity in lamina IV of the striate cortex of Old World monkeys. Exp. Brain Res. 54, 367–372.

- Yotsumoto, Y., Watanabe, T., and Sasaki, Y. (2008). Different dynamics of performance and brain activation in the time course of perceptual learning. Neuron 57, 827–833.
- Shibata, K., Sasaki, Y., Kawato, M., and Watanabe, T. (2016). Neuroimaging evidence for 2 types of plasticity in association with visual perceptual learning. Cereb. Cortex 26, 3681–3689.
- Gilbert, C.D., and Li, W. (2012). Adult visual cortical plasticity. Neuron 75, 250–264.
- Heynen, A.J., Yoon, B.-J., Liu, C.-H., Chung, H.J., Huganir, R.L., and Bear, M.F. (2003). Molecular mechanism for loss of visual cortical responsiveness following brief monocular deprivation. Nat. Neurosci. 6, 854–862.
- Frenkel, M.Y., and Bear, M.F. (2004). How monocular deprivation shifts ocular dominance in visual cortex of young mice. Neuron 44, 917–923.
- Moore, B.D., 4th, Kiley, C.W., Sun, C., and Usrey, W.M. (2011). Rapid plasticity of visual responses in the adult lateral geniculate nucleus. Neuron 71, 812–819.
- Sherman, S.M. (2016). Thalamus plays a central role in ongoing cortical functioning. Nat. Neurosci. 19, 533–541.