

# 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

### Authors

Qinlin Yu, Peng Zhang, Jiang Qiu, Fang Fang

### Correspondence

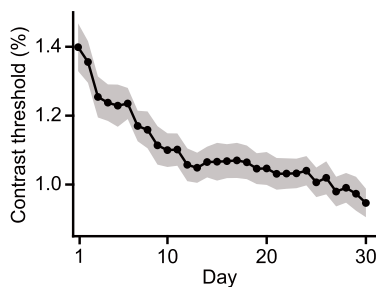
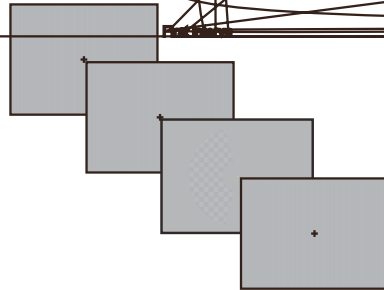
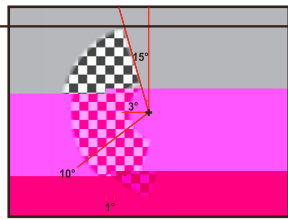
ffang@pku.edu.cn

### 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.

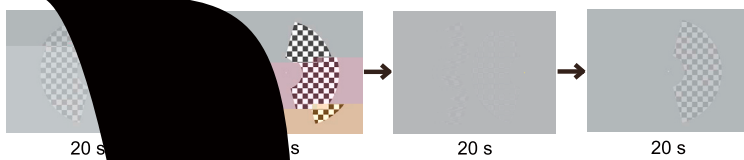




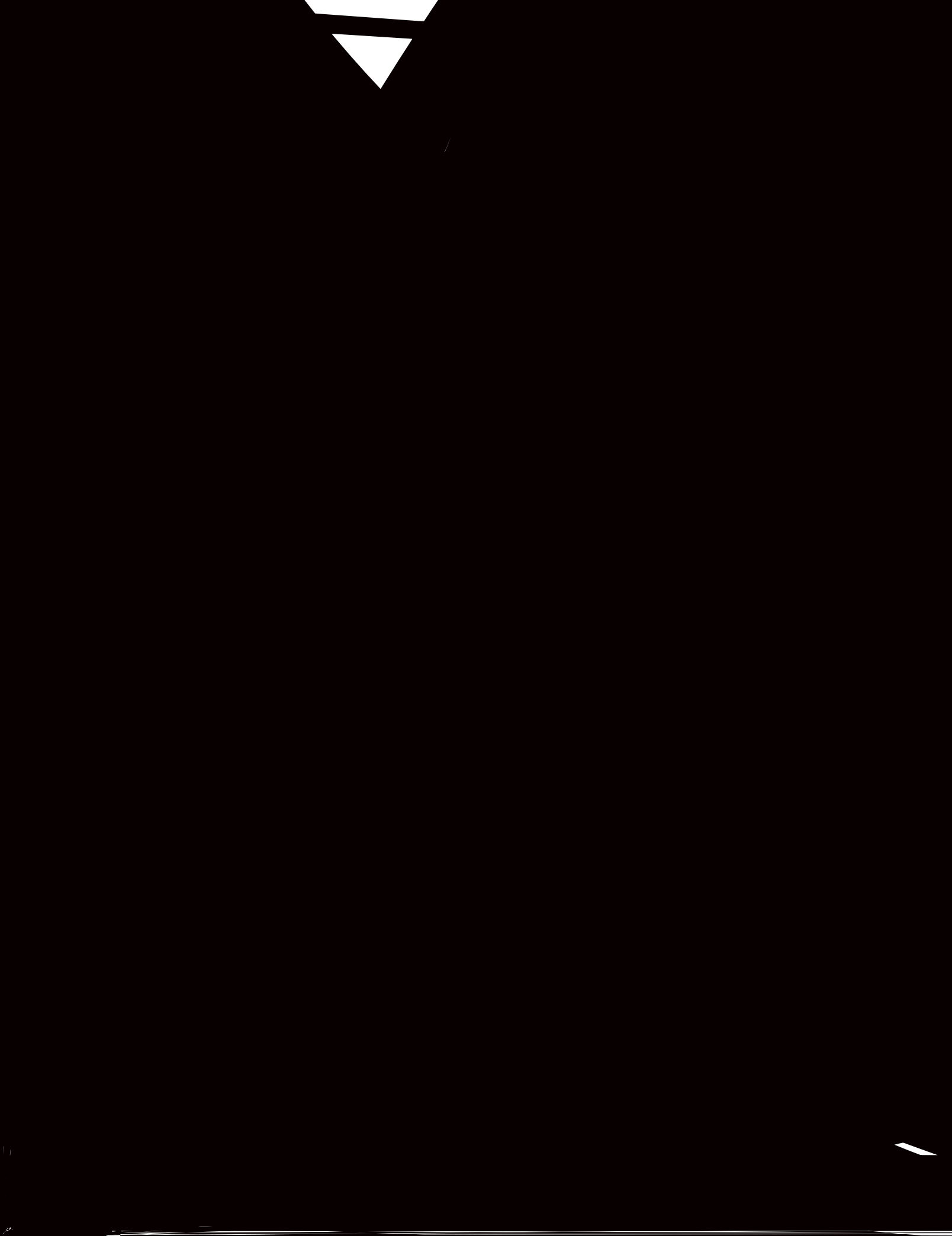


voxels was further constrained by the anatomical locations of the LGN based on high-resolution T1 images. On the T1 images in [Figure 2A](#), which shows the LGN from a representative subject, the LGN appeared darker relative to surrounding brain tissues. The LGN is the thalamic component in the retinocortical 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 (pre- and post-training) and contrast (6%, 24%, and 96%) as within-subject factors. The main effects of contrast were significant (LGN: all  $F_s(2, 38) > 82.82$ ,  $p < 0.001$ ; V1: all  $F_s(2, 38) > 142.77$ ,  $p < 0.001$ ; V2: all  $F_s(2, 38) > 168.93$ ,  $p < 0.001$ ; V3: all  $F_s(2, 38) > 122.98$ ,  $p < 0.001$ , Bonferroni corrected). The BOLD responses increased with contrast. The main effects of training were not significant (LGN: all  $F_s(2, 19) < 3.195$ ,  $p > 0.36$ ; V1: all  $F_s(2, 19) < 0.378$ ,  $p = 1$ ; V2: all  $F_s(2, 19) < 0.445$ ,  $p = 1$ ; V3: all  $F_s(2, 19) < 1.217$ ,  $p = 1$ ). 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 differentially activate M (M stimulus) and P (P stimulus) neurons in 15 of the subjects. The P stimulus was a high-spatial-frequency dominant red/green square wave pattern and was counterphase flickered at 1 Hz. The M stimulus was a low-spatial-frequency sine wave pattern, with 30% luminance contrast and was counterphase flickered at 7.5 Hz (Figure 3A). The M layers of the LGN were identified as voxels showing a greater response to the M stimulus than to the 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 voxels within 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





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.

#### ACKNOWLEDGMENTS

This work was supported by grants NSFC 31230029, MOST 2015CB351800, NSFC 31421003, NSFC 61621136008, and NSFC 61527804.

Received: July 16, 2016

Revised: September 9, 2016

Accepted: September 19, 2016

Published: November 10, 2016

#### REFERENCES

- Sagi, D. (2011). Perceptual learning in vision research. *Vision Res.* 51, 1552D1566
- 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 identification 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, 13678D13683.
- Yan, Y., Rasch, M.J., Chen, M., Xiang, X., Huang, M., Wu, S., and Li, W. (2014). Perceptual training continuously refines 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, 17D29
- Derrington, A. (2001). The lateral geniculate nucleus. *Curr. Biol.* 11, R635D R637.
- 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-field functional magnetic resonance imaging. *Neuron* 32, 359D374
- 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 superficial 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
- Yang, T., and Maunsell, J.H. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *J. Neurosci.* 24, 1617D1626
- 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, 17137D17142
- Chen, N., Cai, P., Zhou, T., Thompson, B., and Fang, F. (2016). Perceptual learning modifies 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, 1867D1888.
- 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

29. 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.
30. 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.
31. 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.
32. Blasdel, G.G., and Fitzpatrick, D. (1984). Physiological organization of layer 4 in macaque striate cortex. *J. Neurosci.* *4*, 880–895.
33. 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.
34. 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.
35. 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.
36. 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.
37. Gilbert, C.D., and Li, W. (2012). Adult visual cortical plasticity. *Neuron* *75*, 250–264.
38. Heynen, A.J., Yoon, B.-J., Liu, C.-H., Chung, H.J., Hugarir, R.L., and Bear, M.F. (2003). Molecular mechanism for loss of visual cortical responsiveness following brief monocular deprivation. *Nat. Neurosci.* *6*, 854–862.
39. Frenkel, M.Y., and Bear, M.F. (2004). How monocular deprivation shifts ocular dominance in visual cortex of young mice. *Neuron* *44*, 917–923.
40. 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.
41. Sherman, S.M. (2016). Thalamus plays a central role in ongoing cortical functioning. *Nat. Neurosci.* *19*, 533–541.