Retinotopically Specific Reorganization of Visual Cortex for Tactile Pattern Recognition

Sing-Hang Cheung,^{1,2,4,*} Fang Fang,^{3,4,*} Sheng He,² and Gordon E. Legge² ¹Department of Psychology The University of Hong Kong Hong Kong China ²Department of Psychology University of Minnesota Minneapolis, MN 55455 USA ³Department of Psychology and Key Laboratory of Machine Perception (Ministry of Education) Peking University Beijing 100871 China

Summary

Although previous studies have shown that Braille reading and other tactile discrimination tasks activate the visual cortex of blind and sighted people [1-5], it is not known whether this kind of crossmodal reorganization is influenced by retinotopic organization. We have addressed this question by studying "S," a visually impaired adult with the rare ability to read print visually and Braille by touch. S had normal visual development until 6 years of age, and thereafter severe acuity reduction due to corneal opacification, but no evidence of visual-field loss. Functional magnetic resonance imaging revealed that, in S's early visual areas, tactile information processing activated what would be the foveal representation for normally sighted individuals, and visual information processing activated what would be the peripheral representation. Control experiments showed that this activation pattern was not due to visual imagery. S's high-level visual areas, which correspond to shapeand object-selective areas in normally sighted individuals, were activated by both visual and tactile stimuli. The retinotopically specific reorganization in early visual areas suggests an efficient redistribution of neural resources in the visual cortex.

Results

Perceptual experience changes the physiological and functional architecture of the developing brain [6]. Brain imaging studies have shown that the visual cortex in blind people is active in Braille reading and other tactile tasks, suggesting crossmodal plasticity [1–5]. Disruption of the visual cortex via transcranial magnetic stimulation (TMS) worsens blind people's performance in both Braille reading and tactile discrimination tasks [3, 7]. However, the precise role of the visual cortex in tactile processing remains controversial. At least two explanations have been suggested for the involvement of the visual cortex in tactile processing. One explanation is that spatial [8–10] or visual [2, 11] imagery plays an important role in the involvement of the visual cortex in tactile tasks in early- and later-blind people. On the other hand, since tactile tasks activate the visual cortex not only in blind people but also in sighted people, the visual cortex has been hypothesized to be a multimodal spatial processor [12, 13]. Short-term visual deprivation by blindfolding sighted people facilitates Braille learning [14] and results in the recruitment of the visual cortex for tactile processing [12, 15, 16]. A potential explanation for this fast crossmodal plasticity is that latent connections between the primary somatosensory cortex and the visual cortex are unmasked when the dominating retinogeniculate visual inputs are blocked.

However, these two explanations do not take into account the functional and spatial organization of the visual cortex. Early visual cortices are known to have retinotopic organization [17, 18]. Neurons representing different retinal eccentricities in the early visual cortices have different spatial frequency tuning [19, 20]. Foveal neurons have a smaller average receptive field size [21, 22] and are more tuned to high spatial frequencies. They are capable of processing visual information at very high spatial frequencies. Cortical neurons representing peripheral vision have larger receptive fields [21, 22] and are more sensitive to the lower range of spatial frequencies.

Visual impairment due to diseases in the early visual pathways often causes acuity reduction and results in selective deprivation of higher spatial frequency inputs to the visual cortex. It is possible that the more severe input deprivation in the foveal cortical regions as compared to the peripheral cortical regions might influence the recruitment pattern of visual cortex for tactile processing. If so, visually impaired people might exhibit a retinotopically specific reorganization of visual cortex in which some regions are retained for visual processing while other regions are reassigned to touch or other sensory modalities.

We report here our findings on "S," a visually impaired person who has the rare ability to read both print visually and Braille by touch. Examination of S's visual cortex via functional magnetic resonance imaging (fMRI) provides a unique opportunity for testing the proposed explanations for tactile processing in visual cortex. If S's impaired vision and skilled Braille reading result in multimodal sharing of the visual cortex, it is important to determine whether the same neurons participate in both vision and touch or whether S's visual cortex exhibits a retinotopically specific segregation of function for vision and touch. Findings on this special case will provide important information about the extent of specificity in crossmodal cortical plasticity.

Case Description

S had normal visual development and acuity until 6 years of age, presumably resulting in normal retinotopic organization in his early visual areas [23, 24]. He then acquired severe bilateral corneal opacification, secondary to Stevens-Johnson syndrome. The vision in his better (right) eye has remained fairly stable since. Clinical examinations showed no evidence of nystagmus in S, and he is capable of stable fixation

^{*}Correspondence: singhang@hku.hk (S.-H.C.), ffang@pku.edu.cn (F.F.) ⁴These authors contributed equally to this work

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Previous studies [4, 29 blind people preferentiall ations, different from the

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agery involves V1 [32] and is retinotopie did not find evidence supporting foveal imagery in S. Nonvisual mental imagery double dissociation in S's visual cortex uble dissociation explained by the hypothcortex is a multimodal spatial processor, t the visual and tactile modalities share the nd activate overlapping regions of the visual tical reorganization studies of blind people ivation studies of blindfolded sighted the unmasking of



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embossed patterns might result in tactile activation of more peripheral portions of S's visual cortex. We believe that this is not the case. In our tactile experiments, we used Braille letters and embossed geometrical shapes, which we believe are typical patterns for tactile processing on the fingertip. Recognizing Braille letters requires the ability to process very fine tactile information. On the other hand, since the geometrical shape stimuli used were at least six times larger in area than Braille letters, much coarser tactile information processing is adequate for making symmetry/asymmetry judgments for these geometrical shapes. Both large (geometrical shapes) and small (Braille) stimuli evoked similar foveal activation and peripheral suppression in the cortex. This finding suggests that the tactile activation of foveal cortex in S was not limited to fine tactile information processing.

Our findings in S may have implications for sight-restoration procedures. What would be the prognosis for S's visual function if a surgical procedure could provide him with good optical image quality? The reorganization of S's visual cortex makes it likely that cortical resources would not be available for highresolution visual analysis even if the retinogeniculate pathway remained capable of encoding high-resolution features. The disappointing visual outcomes after "sight-restoration" surgery reported in the case studies of long-term severe visual impairment by Gregory and Wallace [34], Sacks [35], and Fine et al. [36] are consistent with this possibility (but see also [37]). On the other hand, it remains possible that sight restoration late in life might be accompanied by vision reclaiming some of the cortical areas that it has lost. Data from the rare case studies available to date, although suggestive, are inadequate for a definitive conclusion about the capabilities of the visual system for reorganization following sight restoration in adulthood.

In summary, our study of S has demonstrated a multimodal "visual" cortex with dissociable functions. In the midst of an increasing amount of evidence for a plastic brain, our findings show a remarkably specific cortical adaptation to sensory experience. Despite the retinogeniculate inputs to the early visual areas, it appears that tactile afferent inputs are able to make use of unused portions of visual cortex in a functionally appropriate fashion. We suggest that the division of early visual areas in S reflects an optimal distribution of cortical resources. As Braille reading is a tactile task that requires high spatial resolution, the remapping of the foveal confluence for Braille reading is beneficial. At the same time, the preserved peripheral cortical representation in the early visual areas is adequate for processing the severely blurred retinal inputs.

Supplemental Data

The Supplemental Data include Supplemental Results, Supplemental Experimental Procedures, and five figures and can be found with this article online at http://www.current-biology.com/supplemental/S0960-9822(09) 00885-9.

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References

- Sadato, N., Pascual-Leone, A., Grafman, J., Ibanez, V., Deiber, M.P., Dold, G., and Hallett, M. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. Nature 380, 526–528.
- Buchel, C., Price, C., Frackowiak, R.S., and Friston, K. (1998). Different activation patterns in the visual cortex of late and congenitally blind subjects. Brain 121, 409–419.
- Cohen, L.G., Weeks, R.A., Sadato, N., Celnik, P., Ishii, K., and Hallett, M. (1999). Period of susceptibility for cross-modal plasticity in the blind. Ann. Neurol. 45, 451–460.
- Burton, H., Snyder, A.Z., Conturo, T.E., Akbudak, E., Ollinger, J.M., and Raichle, M.E. (2002). Adaptive changes in early and late blind: A fMRI study of Braille reading. J. Neurophysiol. 87, 589–607.
- Sadato, N., Okada, T., Honda, M., and Yonekura, Y. (2002). Critical period for cross-modal plasticity in blind humans: A functional MRI study. Neuroimage *16*, 389–400.
- Hubel, D.H., and Wiesel, T.N. (1970). The period of susceptibility to the physiological effects of unilateral eye closure in kittens. J. Physiol. 206, 419–436.
- Cohen, L.G., Celnik, P., Pascual-Leone, A., Corwell, B., Falz, L., Dambrosia, J., Honda, M., Sadato, N., Gerloff, C., Catalá, M.D., et al. (1997). Functional relevance of cross-modal plasticity in blind humans. Nature 389, 180–183.
- De Volder, A.G., Toyama, H., Kimura, Y., Kiyosawa, M., Nakano, H., Vanlierde, A., Wanet-Defalque, M.C., Mishina, M., Oda, K., Ishiwata, K., et al. (2001). Auditory triggered mental imagery of shape involves visual association areas in early blind humans. Neuroimage *14*, 129–139.
- Vanlierde, A., De Volder, A.G., Wanet-Defalque, M.C., and Veraart, C. (2003). Occipital-parietal cortex activation during visuo-spatial imagery in early blind humans. Neuroimage 19, 698–709.
- Lambert, S., Sampaio, E., Mauss, Y., and Scheiber, C. (2004). Blindness and brain plasticity: Contribution of mental imagery? An fMRI study. Brain Res. Cogn. Brain Res. 20, 1–11.
- Zhang, M., Weisser, V.D., Stilla, R., Prather, S.C., and Sathian, K. (2004). Multisensory cortical processing of object shape and its relations to mental imagery. Cogn. Affect. Behav. Neurosci. 4, 251–259.
- 12. Pascual-Leone, A., and Hamilton, R. (2001). The metamodal organization of the brain. Prog. Brain Res. *134*, 427–445.
- Merabet, L., Thut, G., Murray, B., Andrews, J., Hsiao, S., and Pascual-Leone, A. (2004). Feeling by sight or seeing by touch? Neuron 42, 173–179.
- Kauffman, T., Theoret, H., and Pascual-Leone, A. (2002). Braille character discrimination in blindfolded human subjects. Neuroreport 13, 571–574.
- Merabet, L.B., Swisher, J.D., McMains, S.A., Halko, M.A., Amedi, A., Pascual-Leone, A., and Somers, D.C. (2007). Combined activation and deactivation of visual cortex during tactile sensory processing. J. Neurophysiol. 97, 1633–1641.
- Merabet, L.B., Rizzo, J.F., Amedi, A., Somers, D.C., and Pascual-Leone, A. (2005). What blindness can tell us about seeing again: Merging neuroplasticity and neuroprostheses. Nat. Rev. Neurosci. 6, 71–77.
- Engel, S.A., Glover, G.H., and Wandell, B.A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. Cereb. Cortex 7, 181–192.
- Dougherty, R.F., Koch, V.M., Brewer, A.A., Fischer, B., Modersitzki, J., and Wandell, B.A. (2003). Visual field representation and locations of visual areas V1/2/3 in human visual cortex. J. Vis. 3, 586–598.
- De Valois, R.L., Albrecht, D.G., and Thorell, L.G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. Vision Res. 22, 545–559.
- Tootell, R.B.H., Silverman, M.S., Hamilton, S.L., Switkes, E., and De Valois, R.L. (1988). Functional anatomy of macaque striate cortex. V. Spatial frequency. J. Neurosci. 8, 1610–1624.

- Smith, A.T., Singh, K.D., Williams, A.L., and Greenlee, M.W. (2001). Estimating receptive field size from fMRI data in human striate and extrastriate visual cortex. Cereb. Cortex *11*, 1182–1190.
- Dumoulin, S.O., and Wandell, B.A. (2008). Population receptive field estimates in human visual cortex. Neuroimage 39, 647–660.
- Martin, E., Joeri, P., Loenneker, T., Ekatodramis, D., Vitacco, D., Hennig, J., and Marcar, V.L. (1999). Visual processing in infants and children studied using functional MRI. Pediatr. Res. 46, 135–140.
- Conner, I.P., Sharma, S., Lemieux, S.K., and Mendola, J.D. (2004). Retinotopic organization in children measured with fMRI. J. Vis. 4, 509–523.
- Talairach, J., and Tournoux, P. (1988). Co-Planar Stereotaxic Atlas of the Human Brain (New York: Thieme Medical Publishers).
- Kourtzi, Z., and Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. Science 293, 1506–1509.
- Fang, F., and He, S. (2005). Cortical response to invisible objects in the human dorsal and ventral pathways. Nat. Neurosci. 8, 1380–1385.
- Amedi, A., Jacobson, G., Hendler, T., Malach, R., and Zohary, E. (2002). Convergence of visual and tactile shape processing in the human lateral occipital complex. Cereb. Cortex 12, 1202–1212.
- Burton, H. (2003). Visual cortex activity in early and late blind people. J. Neurosci. 23, 4005–4011.
- Devor, A., Ulbert, I., Dunn, A.K., Narayanan, S.N., Jones, S.R., Andermann, M.L., Boas, D.A., and Dale, A.M. (2005). Coupling of the cortical hemodynamic response to cortical and thalamic neuronal activity. Proc. Natl. Acad. Sci. USA 102, 3822–3827.
- Shmuel, A., Augath, M., Oeltermann, A., and Logothetis, N.K. (2006). Negative functional MRI response correlates with decreases in neuronal activity in monkey visual area V1. Nat. Neurosci. 9, 569–577.
- Kosslyn, S.M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J.P., Thompson, W.L., Ganis, G., Sukel, K.E., and Alpert, N.M. (1999). The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. Science 284, 167–170.
- Slotnick, S.D., Thompson, W.L., and Kosslyn, S.M. (2005). Visual mental imagery induces retinotopically organized activation of early visual areas. Cereb. Cortex 15, 1570–1583.
- Gregory, R.L., and Wallace, J.G. (1963). Recovery from early blindness: A case study. Exp. Psychological Soc. Monograph 2 (Cambridge: Heffer and Sons).
- Sacks, O. (1995). To see and not see. In An Anthropologist on Mars (New York: Vintage Books, Random House).
- Fine, I., Wade, A.R., Brewer, A.A., May, M.G., Goodman, D.F., Boynton, G.M., Wandell, B.A., and MacLeod, D.I. (2003). Long-term deprivation affects visual perception and cortex. Nat. Neurosci. 6, 915–916.
- Ostrovsky, Y., Andalman, A., and Sinha, P. (2006). Vision following extended congenital blindness. Psychol. Sci. 17, 1009–1014.