

Retinotopically Specific Reorganization of Visual Cortex for Tactile Pattern Recognition

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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 shape- and 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.

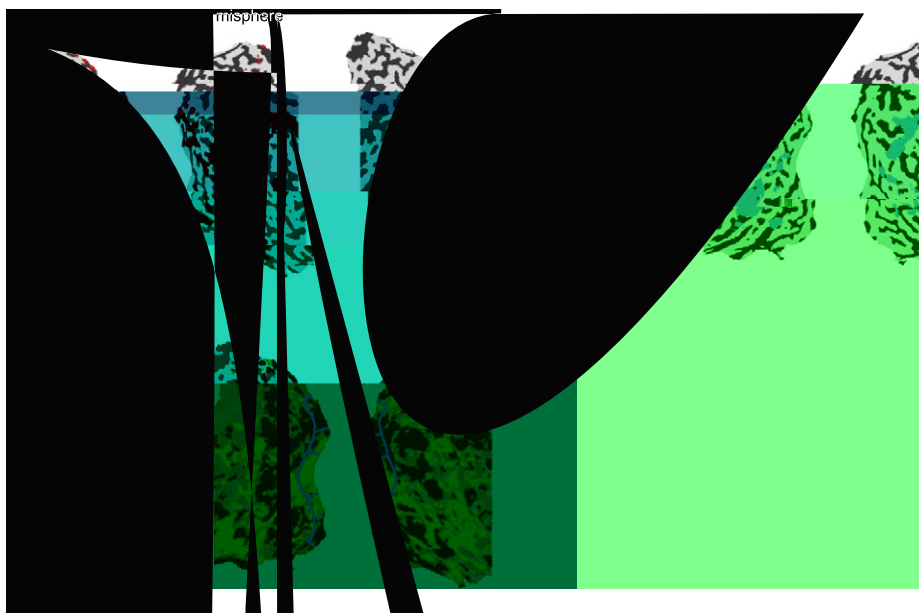
We report here our findings on “S,” a visually impaired person who has the rare ability to read both print visually and Braille by touch. Examination of S’s visual cortex via functional magnetic resonance imaging (fMRI) provides a unique opportunity for testing the proposed explanations for tactile processing 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 cross-modal 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

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also been found to be activated by tactile object perception tasks in normally sighted people [28]. It appears that S's Braille processing finds its way not only into the early visual areas but also into the high-level areas that are normally involved in visual shape perception.

We next asked whether the activation of S's foveal confluence was dependent on the linguistic content of the Braille task. To address this, we measured BOLD response in S while he performed a non-Braille tactile task and its visual counterpart. S was asked to make a symmetry/asymmetry judgment for simple geometrical shapes presented either visually or tactually. This tactile task induced an fMRI activation pattern similar to the map of the Braille task (see Figure 3), suggesting that S's foveal activation to tactile inputs is primarily perceptual processing rather than a top-down linguistic processing specific to Braille reading.

In order to evaluate the possible role of the foveal confluence in the double-dissociation phenomenon in S, we measured S's BOLD response to a spoken word and imagined word (red/green) or case (upper/lower) discrimination task. The results showed a significant correlation between stimulus type and BOLD response in S's foveal confluence (Supplemental Experiment 2, available at www.jneurosci.org as supplemental material). These activations in S's foveal confluence were outside the area of significant activation in S's high-level visual areas. In addition, the activation in S's high-level visual areas occurred only when he was asked to discriminate tactile details.

to activate V1, but it was not sufficient to activate V1 in S during the tactile task.

Control Experiment 1: Tactile and Visual Discrimination Task
All normally sighted people have a foveal confluence that is specialized for high-resolution visual processing. To simulate the tactile processing in S, we used a tactile discrimination task that required fine-grained tactile processing.

In this task, subjects were asked to discriminate between two stimuli (e.g., red/green or case/upper/lower) presented either visually or tactually. The results showed that the tactile task induced an fMRI activation pattern similar to the map of the Braille task (see Figure 3), suggesting that S's foveal activation to tactile inputs is primarily perceptual processing rather than a top-down linguistic processing specific to Braille reading.

The results of the control experiment show that experience-specific cortical specialization can be remarkably specific. The foveal confluence in S had ceased to deliver fine-grained visual processing after 6 years of age. Even though S was adept at resolving visual details, he was not adept at resolving tactile details. The results suggest that S's foveal confluence continued to process coarse-grained visual information. We interpret our findings as evidence that the experience-specific cortical reorganization is determined by both the availability of input and the functional specialization of the cortex.

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 high-resolution 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](http://www.current-biology.com/supplemental/S0960-9822(09)00885-9).

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