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Report

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 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

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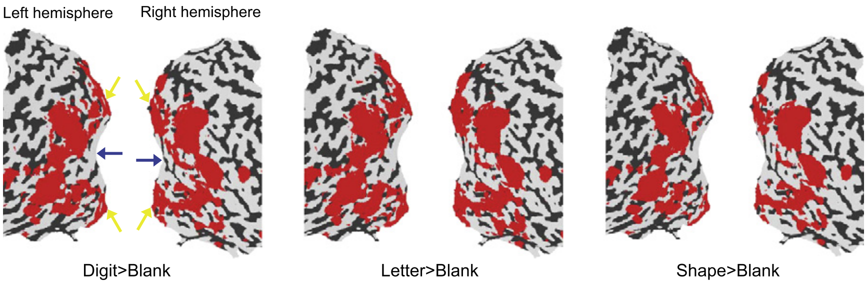


Figure 1. **fMRI Activation Maps by Visual Stimuli in S**

Statistical significance maps (thresholded at corrected $p < 0.01$) are shown on a flattened surface reconstruction of the posterior part of S's brain. Red regions were activated by visually presented digits (left), letters (middle), and shapes (right) contrasting with blank intervals. S's foveal and peripheral representations in V1 are indicated by blue and yellow arrows, respectively.

(see Figures S1 and S2 available online). Photopic electroretinograms showed no retinal defects in S, and a tangent-field test confirmed that there was no central-visual-field loss (Figure S3).

At the time of testing, at 56 years of age, S had Snellen acuity of 20/1000, Pelli-Robson contrast sensitivity of 1.00 log unit, and a full visual field. S is a university professor who reads highly magnified print on a daily basis at tested speeds from 44 to 100 words per minute. He started to read Braille at 7 years of age and is a competent Braille reader, reading daily at a tested speed of 110 words per minute.

Lack of Activation in S's Foveal Confluence by Visual Stimuli

Blood oxygen level-dependent (BOLD) response to different stimuli was measured by fMRI. We attempted retinotopic mapping in S by using variants of a standard technique. We presented four 3° thick annuli at eccentricities of 1.5°, 4.5°, 7.5°, and 10.5° and four 45° wedges with a radius of 12° at the horizontal and vertical meridians. However, the resulting fMRI activation maps failed to reveal retinotopic maps in S's occipital cortex. Instead, these stimuli produced activation maps similar to a 26° disk stimulus (Figure S4). It is likely that S's cornea produced sufficient light scatter across S's retina to render the retinotopic mapping stimuli ineffective. Therefore, the visual areas of S's cortex were identified mainly by their anatomical locations [18, 25].

Figure 1 shows the regions that were activated by visually presented digits, letters, and simple shapes when S performed a categorization task. These three kinds of stimuli induced similar patterns of cortical activations in both hemispheres: the visually activated regions formed a band that surrounded the occipital pole, but the occipital pole was not activated. A similar pattern was also observed when S passively viewed a flickering red/green disk, a flickering black/white disk, or moving dots (Figure S4).

The visually inactive and active regions in S's visual cortex closely match the foveal and peripheral representations in the early visual areas, respectively [18] (note that the active regions also include some high-level visual areas extending into temporal and parietal lobes). Since S had no central-visual-field loss, the lack of activity in the foveal confluence is surprising.

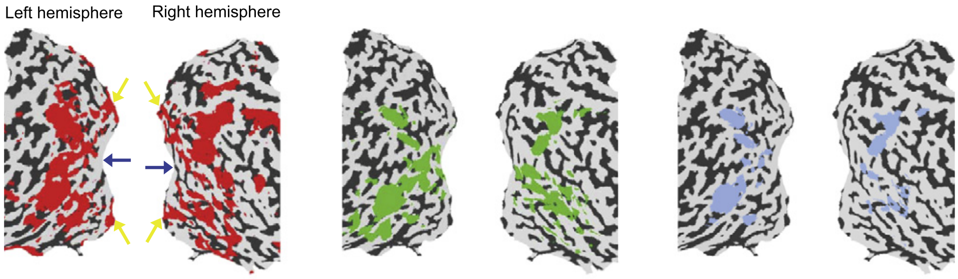
S's retina receives a severely blurred and low-contrast image due to the degraded optics of his eyes. Due to the different spatial frequency tuning properties of foveal and peripheral neurons [17–22], the loss of high spatial frequency content might result in a preferential activation of the peripheral cortical regions representing peripheral vision during visual stimulation. We tested this idea by measuring cortical response to various visual stimuli in normally sighted control participants who wore diffuser goggles that simulated S's retinal image quality. The foveal confluence of these normally sighted controls was activated during visual stimulation (see Figure S4). Therefore, we conclude that the foveal confluence in S has been disengaged from normal processing of visual information.

Double Dissociation in S's Early Visual Areas

We then studied S's cortical activity during both visual and Braille lexical decision tasks. S read Braille letter strings of three characters and indicated whether each of the strings was a word. S also performed the same lexical decision task with highly magnified visually displayed letter strings. The Braille task and the visual task were performed within the same fMRI scans, in different blocks separated by blank rest periods. Figure 2 shows the fMRI activation maps indicating the BOLD contrast between each stimulus condition and the blank condition (upper left and upper middle panels) and the contrast between the Braille and the visual lexical decision conditions (lower left panel). Red and green regions indicate stronger BOLD response to the visual task and the Braille task, respectively. The foveal confluence is preferentially activated during the Braille task. The peripheral cortical representation is preferentially activated during the visual task.

Three contiguous regions of interest (ROIs) with roughly the same size were defined along the calcarine sulcus (see the lower left panel of Figure 2), including its lower and upper banks, where early visual areas V1/V2 are usually found. These three ROIs would presumably have corresponded to S's fovea (0°–1.5°), parafovea (1.5°–5°), and periphery (5°–12°) if there had been no cortical reorganization. The Talairach coordinates [25] of the fovea ROI are close to a previous measurement in normally sighted individuals [18]. In line with the cortical activation maps, the BOLD signals evoked by the Braille task and the visual task relative to the blank intervals showed opposite trends from fovea to periphery (lower right panel of Figure 2). The BOLD signals were elevated during the Braille task at the foveal confluence and the visual task at the peripheral representation, but the BOLD signals were suppressed during the Braille task at the peripheral representation and the visual task at the foveal confluence. The foveal activation by the Braille task seemed to show a tendency for left lateralization, consistent with a report by Burton and colleagues [4].

In addition to the double dissociation in early visual areas, we also found a sharing of cortical resources between Braille reading and visual tasks in other visual areas. The light blue regions in the upper right panel of Figure 2 were activated during both the Braille and the visual lexical decision tasks. The shared regions are located in dorsal and lateral occipital areas, ventral occipitotemporal areas, and intraparietal sulcus, which closely match the reported locations of visual object- and shape-selective areas [26, 27]. Some visual object- and shape-selective areas (e.g., lateral occipital complex) have



Visual letter string>Blank

Braille>Blank

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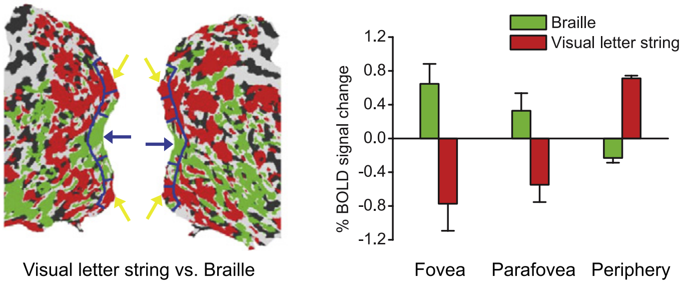


Visual letter string vs. Braille

Figure 2. fMRI Activation Maps by Visual Letter String and Braille in S

Statistical significance maps (thresholded at corrected $p < 0.01$) are shown on a flattened surface reconstruction of the posterior part of S's brain. Upper left: red regions were activated by visual letter strings contrasting with blank intervals. Upper middle: green regions were activated by Braille contrasting with blank intervals. Upper right: light blue regions were activated by both visual letter strings and Braille contrasting with blank intervals. Lower left: visual letter string and Braille conditions were contrasted with each other. Red regions showed higher response to visual letter strings than to Braille, and green regions showed the opposite. S's foveal and peripheral representations in V1 are indicated by blue and yellow arrows, respectively. Lower right: blood oxygen level-dependent (BOLD) signals evoked by Braille and visual letter strings relative to blank intervals in three V1 subregions (Talairach coordinates shown in parentheses): fovea (left: −21, −95, −4; right: 17, −95, −8), parafovea (left: −6, −94, −9; right: 4, −92, −7), and periphery (left: −5, −75, −6; right: 3, −75, −1). The three subregions are delineated by blue curves in the lower left panel. Error bars denote one standard error of the mean across scans.

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 map similar to the map of the Braille task (see Figure 3), suggesting that S's foveal activation to tactile inputs is due to tactile perceptual processing rather than a top-down influence from linguistic processing specific to Braille reading.

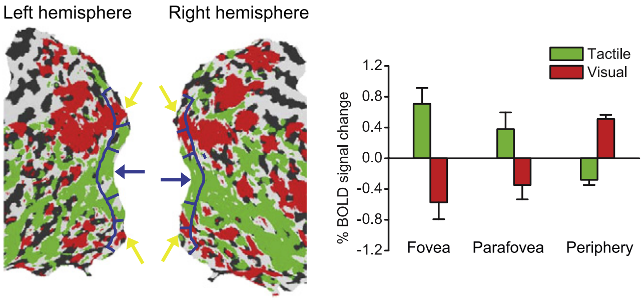
In order to evaluate the possible role of visual imagery in this double-dissociation phenomenon in S's early visual cortex, we measured S's BOLD response to a visual imagery task. S heard a spoken word and imagined the word in a prespecified color (red/green) or case (upper/lower). (We equated auditory stimulation between stimulus blocks and blank blocks. See Supplemental Experimental Procedures.) We found sporadic activations in S's early visual cortex in this task, but they were outside of S's foveal confluence (left panel of Figure 4). In addition, the imagery task produced substantial activations in S's high-level visual cortex, including the dorsal and lateral occipital areas, ventral occipitotemporal areas, and intraparietal sulcus, which significantly overlapped with the areas activated by the Braille task (right panel of Figure 4). It should be noted that our visual imagery task might not be the best one to activate V1, but it was designed to best match the Braille task.

Control Experiments with Normally Sighted Participants

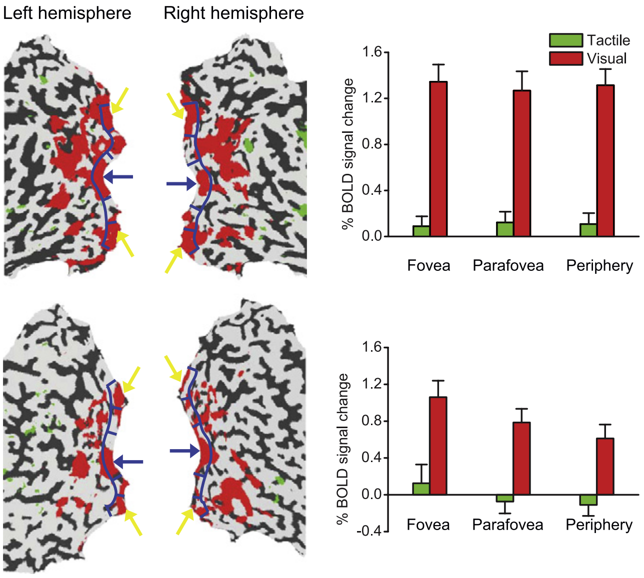
All normally sighted control participants wore diffuser goggles to simulate S's retinal image quality during fMRI testing. The diffuser goggles reduced their Snellen acuity to 20/1000, approximately matching S's visual acuity. Two young controls (26 and 27 years old) participated in the visual and Braille lexical decision scans. Since the young controls could not read Braille, they were asked to feel the Braille symbols and to count the dots, instead of performing the Braille lexical decision task. Two age- and gender-matched controls (males aged 56 and 59 years) participated in the same visual and tactile shape categorization scans as S. In all control participants, we found no evidence for tactile activation of the foveal confluence (Figure 3; Figure S5).

Discussion

Our findings in S show that experience-dependent cortical reorganization can be remarkably specific. S's retinogeniculate pathway ceased to deliver fine-grained visual information to his visual cortex after 6 years of age. Eventually, the neurons normally adept at resolving visual details were recruited for fine discrimination of tactile details. The rest of the visual neurons continued to process coarse visual information. Thus, we interpret our findings as evidence for a visual and tactile experience-specific cortical reorganization that is guided by both the availability of input information and the inherent functional specialization of the neurons involved.



From S



From two age-matched participants

Figure 3. fMRI Activation Maps by Visual and Tactile Shapes in S and Two Age-Matched Control Participants

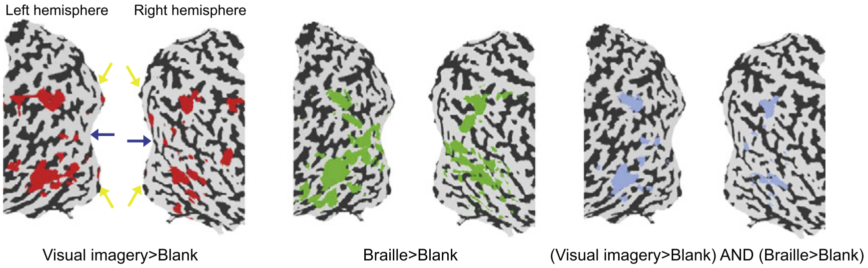
Statistical significance maps (thresholded at corrected $p < 0.01$) are shown on a flattened surface reconstruction of the posterior part of participants' brains. Left: visual shape and tactile shape conditions were contrasted with each other. Red regions showed higher response to visual shape than to tactile shape, and green regions showed the opposite. Participants' foveal and peripheral representations in V1 are indicated by blue and yellow arrows, respectively. Right: BOLD signals evoked by tactile and visual shapes relative to blank intervals in three V1 subregions (fovea, parafovea, and periphery), which are delineated by blue curves on the flattened surfaces at left. Error bars denote one standard error of the mean across scans.

S's early exposure to the high tactile spatial resolution demanded by Braille reading and other tactile tasks might have been the trigger for crossmodal "takeover" of the foveal representation. His visual cortex has responded to the development of skills in tactile pattern analysis, especially Braille reading, and the concomitant experience of partial visual deprivation by reorganizing crossmodally at the foveal confluence.

Previous studies [4, 29] have found that Braille reading in blind people preferentially recruited their peripheral representations, different from the foveal activation in S. This might be due to S's special visual and tactile experience, and perhaps to different study designs as well. Accompanying the foveal activation by tactile stimuli and the peripheral activation by visual stimuli in S, there were corresponding peripheral and foveal suppressions of BOLD signal. Negative BOLD signals are pervasive in functional brain imaging studies, but their origin remains controversial [30, 31]. Whether the negative BOLD signals in S are an epiphenomenon or have a functional role remains unresolved.

Although visual imagery involves V1 [32] and is retinotopically specific [33], we did not find evidence supporting foveal activation by visual imagery in S. Nonvisual mental imagery cannot explain the double dissociation in S's visual cortex either. Nor is this double dissociation explained by the hypothesis that the visual cortex is a multimodal spatial processor, which predicts that the visual and tactile modalities share the neural resources and activate overlapping regions of the visual cortex. Unlike cortical reorganization studies of blind people [1–5] or visual deprivation studies of blindfolded sighted people [12, 15], our results indicate that the unmasking of connections between the somatosensory cortex and visual cortex can be very specific and functionally adaptive. The recruitment of the visual cortex for touch seems optimal: only those visual neurons that are not critical for S's remaining low-resolution vision are recruited for tactile processing.

We considered two possible artifactual explanations based on stimulus size for the activation and suppression pattern in S's visual cortex. First, because most of our visual stimuli covered a large portion of the field, it might be argued that stimulation of both foveal and peripheral regions of the visual field could lead to competitive interaction between these regions in the cortex and result in foveal suppression by peripheral cortical responses. A related argument is that S attended only to the global outline of large stimuli, accounting for peripheral activation and foveal suppression. But S's data from the retinotopic mapping experiment counter these explanations. In this experiment, a small annulus and a large annulus activated the same peripheral area in S's cortex, and attending to a small stimulus did not selectively activate S's foveal projection. Also, S's ability to read printed text implies that he pays attention to internal features as well as bounding contours of patterns. Second, it might be argued that Braille symbols are physically small, and stimulation with larger



Visual imagery>Blank

Braille>Blank

(Visual imagery>Blank) AND (Braille>Blank)

Figure 4. fMRI Activation Maps by Visual Imagery and Braille in S

Statistical significance maps (thresholded at corrected $p < 0.01$) are shown on a flattened surface reconstruction of the posterior part of S's brain. Left: red regions were activated by visual imagery contrasting with blank intervals. Middle: green regions were activated by Braille contrasting with blank intervals. Right: light blue regions were activated by both visual imagery and Braille contrasting with blank intervals. S's foveal and peripheral representations in V1 are indicated by blue and yellow arrows, respectively.

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.

Acknowledgments

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