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Report

A Ventral Visual Stream Reading Center Independent of Visual Experience

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Summary

The visual word form area (VWFA) is a ventral stream visual area that develops expertise for visual reading [1–3]. It is activated across writing systems and scripts [4, 5] and encodes letter strings irrespective of case, font, or location in the visual field [1] with striking anatomical reproducibility across individuals [6]. In the blind, comparable reading expertise can be achieved using Braille. This study investigated which area plays the role of the VWFA in the blind. One would expect this area to be at either parietal or bilateral occipital cortex, reflecting the tactile nature of the task and crossmodal plasticity, respectively [7, 8]. However, according to the metamodal theory [9], which suggests that brain areas are responsive to a specific representation or computation regardless of their input sensory modality, we predicted recruitment of the left-hemispheric VWFA, identically to the sighted. Using functional magnetic resonance imaging, we show that activation during Braille reading in blind individuals peaks in the VWFA, with striking anatomical consistency within and between blind and sighted. Furthermore, the VWFA is reading selective when contrasted to high-level language and low-level sensory controls. Thus, we propose that the VWFA is a metamodal reading area that develops specialization for reading regardless of visual experience.

Results

Activation of the Visual Word Form Area during Braille Words Reading in the Congenitally Blind

In order to investigate whether the visual word form area (VWFA) is activated while reading words regardless of sensory modality and visual experience, we used functional magnetic resonance imaging (fMRI) to image the neural activity in eight congenitally blind subjects while reading via touch using Braille. Before statistical analysis, standard preprocessing procedures were performed (see [10] and the Supplemental Information available online for detailed experimental procedures). For the main contrast of Braille words reading versus nonsense Braille, data were analyzed on several levels using various approaches: (1) region of interest (ROI) analysis in the sighteds' VWFA, (2) whole-brain group analysis, (3) probabilistic mapping showing the consistent activations across individuals, and (4) distribution plot of blind and sighted individuals' peaks, based on single-subject analysis.

We first looked at the blinds' pattern of activation in the VWFA ROI, as reported originally in sighted subjects ([11]; Talairach coordinates [TC] [12] −42, −57, −6). The result was clear cut: we found a highly significant preference for Braille words over nonsense Braille stimuli in the canonical left-hemispheric VWFA ($p < 10^{-7}$, $t = 9.270$; Figure 1A).

We next investigated whether the VWFA is the main peak of activation or whether it is just one of many brain areas more responsive to Braille words than to nonsense Braille. To this end, we performed a whole-brain analysis of this contrast, masked by voxels that were significantly activated by Braille words versus baseline (thus discarding areas showing negligible activation or even deactivation to Braille words but a larger deactivation to nonsense Braille). We found robust activation in the entire left ventral occipitotemporal cortex all the way to V1 (Figure 1B; see [13–15]). Critically, the blind group's peak of activation (i.e., the most significant cluster across the entire brain) was located specifically in the occipitotemporal sulcus, at coordinates practically identical to those reported in sighted (Figures 1B and 1C; blind TC −38, −60, −8; sighted TC −42, −57, −6; the difference between the two groups' peaks was within 1−2 functional voxels in all axes). Thus, the VWFA is the area most selective to reading, independent of the modality in which words are presented.

Anatomical Selectivity and Reproducibility of the Blinds' VWFA across Individual Subjects

A key characteristic of the sighteds' VWFA is its high reproducibility across individual subjects [6]. Is it also reproducible in the blind? To answer this, we created a probabilistic map (Figure 2A) showing the overlap and reproducibility between all individual blind subjects for the main contrast. The coordinates of the most consistent area across the entire brain, activated in 100% of our blind subjects, were again virtually identical to the sighteds' VWFA peak (blind TC −39, −59, −7; sighted TC −42, −57, −6).

We further explored this reproducibility by plotting all individual subjects' peaks for the main contrast, sampled using the same criterion reported in the sighted ([16]: the individual subject peak closest to the group analysis peak). The plot clearly showed that all individual peaks were very closely packed around the occipitotemporal sulcus (Figure 2B, marked in red circles). Interestingly, the variance in the peak locations among the blind was very small in all three axes and was similar to that of the sighted, with a trend for even smaller variance in the blind in the y and z axes (sighted data from [16]; standard deviation: blind $x = 3.4$, $y = 3.6$, $z = 3.3$; sighted $x = 3.4$, $y = 5.4$, $z = 5.8$).

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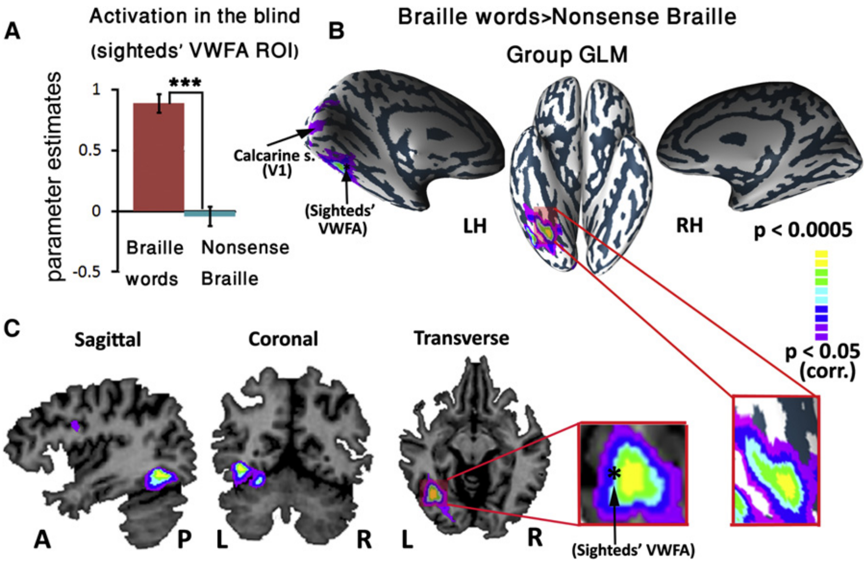

Figure 1. Visual Word Form Area Is the Peak of Braille Words Reading Activation across the Entire Brain of the Congenitally Blind

(A) The parameter estimates of blind subjects' activations for Braille words and nonsense Braille conditions, sampled from sighteds' visual word form area (VWFA) region of interest (ROI). During Braille word epochs, subjects were instructed to covertly read abstract Braille words. In the nonsense Braille condition, subjects swept their reading finger over a surface homogenously covered by a repeated full six-dot Braille sign (which is not part of the Braille alphabet) and were instructed to maintain the same sweep speed as in reading Braille words. The activation shows a highly significant preference for Braille words ($p < 10^{-7}$, $t = 9.270$). Error bars represent standard error of the mean.

(B and C) Statistical parametric map calculated using across-subjects ($n = 8$) hierarchical random effects general linear model [49] for the contrast of Braille words versus nonsense Braille, presented on an inflated brain (B) and on brain sections (C). Activation was found in the "visual" ventral stream, with the peak of activation in the VWFA. We used a statistical threshold criterion of $p < 0.05$ corrected for multiple comparisons across the entire brain (for more details, see Supplemental Experimental Procedures).

To further explore the consistency between the blind and sighted populations, we plotted together the peaks of all individuals from both groups (sighted data from [16]; Figure 2B). The left panel represents all subjects without a group tag, demonstrating that the groups cannot be distinguished by simple examination of the peaks' distribution; the right panel includes a group tag for each individual. For the purpose of illustration, we conducted a k-means clustering analysis, which in our case was designed to partition $n = 24$ observations (16 sighted, 8 blind) into $k = 2$ clusters, so as to minimize the within-cluster sum of squares [17]. Both clusters show a mixture of peaks of both blind and sighted individuals rather than a distinct anatomical cluster for each population (Figure 2C). To statistically test the contribution of the group factor to the variance, we conducted a multivariate analysis of variance (MANOVA) with three dependent variables, one for each axis [18]. The populations were statistically indistinguishable in the y ($p > 0.1$, $F < 3$) and z ($p > 0.05$, $F < 3.5$) axes, whereas in the x axis there was a quantitatively small effect (4 mm difference) that clearly reached significance ($p < 0.005$, $F > 9$). Note that the difference between the average peak (based on the single-subject peaks) of the two groups was very small (less than 2 functional voxels in all axes; 4 mm in the x and z; 3 mm in the y). Note that both the k-means and the MANOVA yielded this very small difference between the blind and sighted individuals' VWFA locations, in spite of additional external factors that are likely to increase the variance between the groups (e.g., the use of different scanners).

Finally, another characteristic of the sighteds' VWFA is its anatomical invariance to reading across the left and right visual fields [11]. In line with this, we found consistent left-lateralized VWFA activation in all blind subjects, even though they read Braille using different hands (see Table S1).

Functional Selectivity of the VWFA to Braille Reading

Previous studies in the blind showed that the entire visual cortex, peaking in V1, is taken over by language-related semantic functions [19], e.g., verb generation (VG), a task that entails understanding a heard noun word and covertly generating a corresponding verb [20]. Therefore, as a supplemental analysis, we studied whether the activation in the VWFA ROI during Braille reading was significantly larger than during VG, each relative to its low-level control condition (nonsense Braille and verb generation control [VGc], respectively). Namely, we tested the interaction between sensory modality (written versus heard) and cognitive processing (perceptual versus language-related). The activation for Braille words versus nonsense Braille was significantly higher than for VG versus VGc ($p < 0.005$, $t > 2.5$; Figure 2D). This suggests that the VWFA is specific to reading and that its activation during Braille reading cannot be reduced to modality-independent general language processing.

Discussion

The VWFA as a Metamodal Area

According to the canonical view, the cortex can be divided into unimodal areas, which process information from one specific sensory modality, and higher-order multimodal integration areas (reviewed in [21]). The metamodal theory of brain function [9] challenges this view and suggests that all brain regions, including those commonly considered unimodal (e.g., the "visual" VWFA), are essentially characterized by the representation or computation that they support or the task that they perform rather than by their main input sense. Support for this theory has come from findings showing that an area in the ventral visual stream, the lateral occipital tactile-visual area (LOtv), is responsive to objects' shape regardless of the input sensory modality and/or visual experience [10, 22–24]. Similarly, the middle occipital gyrus has been shown to be a metamodal operator for spatial localization [25]. Additionally, it has been demonstrated that the animate-inanimate organization of the ventral visual cortex prevails independently of input modality and visual experience [26]. In the present study,

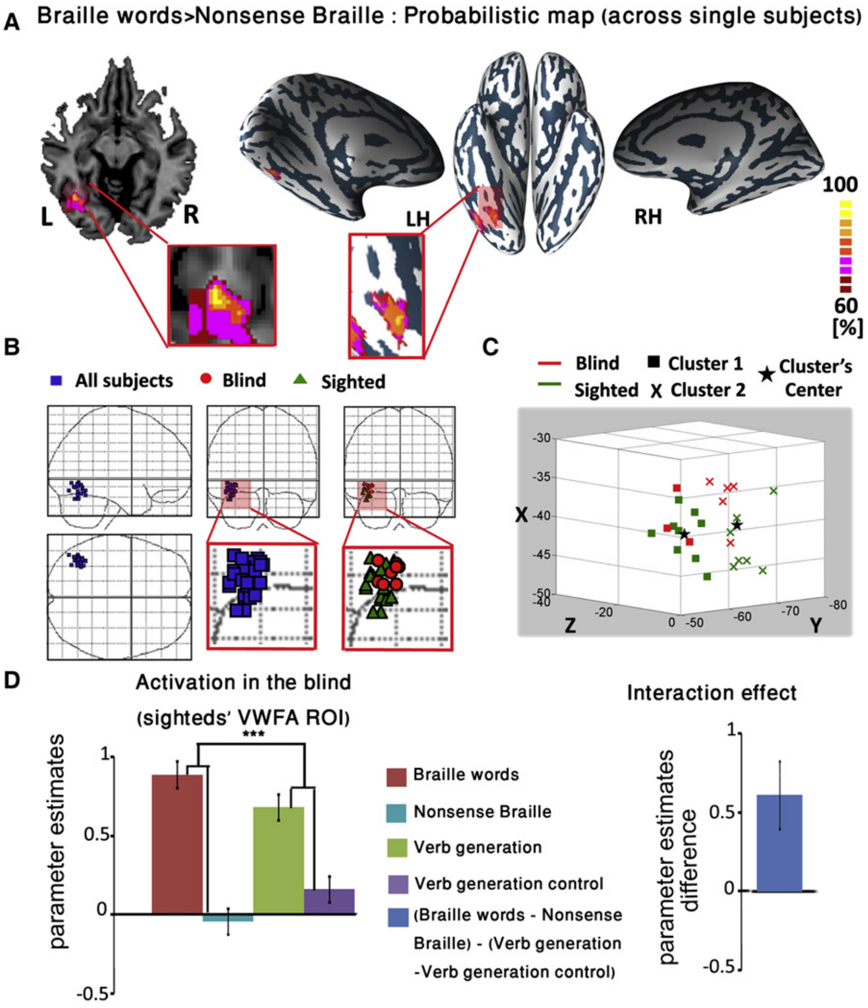

Figure 2. VWFA Is Reading Selective and Shows Astonishing Anatomical Consistency within the Blind Group, and Also between Blind and Sighted Individuals

(A) Probabilistic map for the contrast of Braille words versus nonsense Braille (same contrast as in the group-level analysis in Figure 1), based on the statistical parametric maps of all individual blind subjects independently ($p < 0.05$ corrected). The map shows the overlapping clusters across a determined percent of subjects. The most consistently activated voxels (activated in 100% of blind subjects) are in the VWFA.

(B) Plot of individual peak activations, demonstrating the spatial reproducibility of the VWFA in blind (current study) and sighted (data from [16]) subjects. At left, all subjects' peaks (both blind and sighted) are represented by blue squares. Note the overlap of the two groups of subjects. At right, there is a group tag (blind or sighted; red circles and green triangles, respectively) for each individual.

(C) k-means clustering of the 24 individual peaks into k = 2 clusters. Red and green represent blind and sighted individuals, respectively; squares and Xs represent the two resulting clusters; a black star marks the center of each cluster. Both clusters contain peaks of both blind and sighted. This analysis and the multivariate analysis of variance (see Results; for more details, see Supplemental Experimental Procedures) further support the anatomical consistency between blind and sighted.

(D) Parameter estimates of blind subjects' activations for Braille words, nonsense Braille, verb generation (VG), and verb generation control (VGc) conditions, sampled from sighteds' VWFA ROI. In VG, subjects heard a noun and covertly generated a corresponding verb. In VGc, subjects heard noise sounds and performed a one-back task. Each noise matched a noun from the VG condition in duration, average amplitude, and temporal envelope by multiplying the epoch's spectrum by the noun's temporal envelope. The interaction contrast of (Braille words − nonsense Braille) − (verb generation − verb generation control) was highly significant, suggesting that the VWFA in the blind is most selective to reading. Error bars represent standard error of the mean.

we put the metamodal theory to a critical test. All of our subjects were congenitally blind and hence had no visual experience during development or familiarity with visual reading. Nevertheless, we showed selective activations to Braille words at the VWFA ROI (Figure 1A; Figure 2D; the VWFA was actually the most significant area across the entire brain; see Figures 1B and 1C), high anatomical reproducibility of the VWFA within and between blind and sighted subjects (Figures 2A–2C), and left lateralization regardless of the reading hand (analogous to the invariance across visual fields). Thus, the main functional properties of the VWFA as identified in the sighted are present as well in the blind and are thus independent of the sensory modality of reading, and even more surprisingly do not require any visual experience. To the best of our judgment, this provides the strongest support so far for the metamodal theory. Hence, the VWFA should also be referred to as the tactile word form area, or more generally as the (metamodal) word form area.

The metamodality of the VWFA (for simplicity, we maintain this abbreviation in the Discussion) fits with views of brain function that emphasize the predictive coding of sensory input rather than the sensory features of stimuli [27, 28]. For instance, it has been shown [29] that the activation of the fusiform face area, an equivalent of the VWFA specialized for face perception, depends on subjects' expectations and on the mismatch between those expectations and the actual sensory input, but not on whether stimuli actually depict faces or houses. Similarly, the VWFA might predict the sensory consequences of words. The metamodality of the VWFA can explain its ability to apply top-down predictions to both visual and tactile stimuli.

Written-Word Processing Chain along the Ventral Occipitotemporal Cortex

Next, we discuss the large-scale organization of the ventral occipitotemporal cortex, integrating the current findings with previous literature. Braille reading has been shown to involve an extended strip of visual cortex stretching from V1 to anterior higher-order regions, probably reflecting a combination of the various components of reading [13–15, 30]. For instance, previous studies focused on the functional relevance of the occipital pole for single-Braille-letter identification [14] or the recruitment of V1 for somatosensory processing [13] or used a task that combined Braille reading with higher-order language processing [30]. However, this is the first study testing directly the role of the VWFA for word form processing, showing that Braille words not only significantly activate the VWFA but peak in the VWFA.

Another related study, carried out by Büchel and colleagues [15], focused specifically on the semantic component of reading by contrasting meaningful words versus meaningless letter strings in both blind and sighted. The peak of activation in both groups was anterior to the VWFA by about 2 cm (Büchel's peak TC −36, −40, −20; blinds' VWFA peak TC −38, −60, −8). Interestingly, previous studies in the sighted have suggested a visual anterior-posterior word processing chain along the left ventral occipitotemporal cortex, with preference for semantics anteriorly and word form posteriorly [31–33]. The combination of our results and the findings reported by Büchel et al. [15] suggest that at least two distinct areas along this processing chain are actually metamodal: the posterior reading-specific VWFA and the anterior associative semantic areas. This supports the notion that the same anatomical organization and reading mechanisms are largely shared by both blind and sighted populations, further supporting the metamodal theory.

How Does Tactile Information Reach the VWFA, and How Does VWFA Project Back?

The activation of the VWFA by tactile reading raises two main questions regarding the routes through which somatosensory information reaches the VWFA and how the VWFA projects back to predict or modulate the somatosensory input (see above). The related connectivity literature in humans is sparse and not decisive. Previous studies suggest at least three potential bottom-up pathways:

(1) A thalamocortical pathway, involving rerouting of the information between thalamic nuclei, as in the blind mole rat [34].

(2) Corticocortical connections between somatosensory cortex and V1, as supported by recent primate studies [7, 35–37]. Some of these connections, which generate multisensory responses in the "unisensory" primary sensory cortex, might exist in the normally developed brain [7, 35] and could be enhanced or unmasked in the absence of visual input, as revealed in blindfolded sighted individuals [9, 38]. In the blind, the constant flow of somatosensory information might strengthen such cross-modal connections using Hebbian mechanisms [38].

According to these two bottom-up options, tactile information would be relayed in V1 before being processed in the VWFA. One may speculate that V1 computes simple geometrical features of Braille letters, comparable to its role in processing line orientation and edge detection during vision. This is supported by studies showing causal involvement of V1 in single-letter identification of Braille signs [14, 38]. From V1, information might continue to flow in the ventral "visual" stream up to the VWFA.

(3) The third bottom-up option is direct corticocortical connections between high-order somatosensory areas and VWFA. If such connections exist, they would be comparable to the connections reported for metamodal shape processing between the intraparietal sulcus and the LOtv [39].

Regarding the backward-predictive or modulatory projections from the VWFA on the sensory input, there is less relevant direct evidence, so one can only speculate. However, it is clear that such top-down backward connections are extremely important in the primate brain. For instance, there are 10–20 times more feedback projections from primary visual cortex to the lower-level visual thalamus (V1 to lateral geniculate nucleus) than there are corresponding feed-forward bottom-up connections [40]. This is true also for higher-order "visual" areas (e.g., between V4 and V1 [40]). Feedback projections have also been demonstrated anatomically between visual areas and somatosensory cortex [41]. Similarly, a recent study in humans has shown bidirectional functional connectivity between LOtv in the ventral stream and somatosensory areas [39]. It is clear that additional anatomical and functional connectivity studies, as well as time-resolved techniques, are needed to establish which of the above routes and mechanisms actually prevail.

Implications for the Origin of the VWFA

Reading is a recent invention (visual reading was invented about 5400 years ago, and Braille has been in use for less than 200 years), so there has not been enough time or selection pressure for the evolution, in the biological sense, of a dedicated brain module. Thus, reading relies on existing brain structures and functions. Several hypotheses have been put forward to account for the inherent biases predisposing the VWFA to be consistently recruited for reading.

One possibility is that these biases are visual in nature. The area that eventually harbors the VWFA would originally perform a specific type of computation particularly suitable to the encoding of written material. Such computation might be based on viewpoint-invariant line junctions, shape features that are particularly useful for reading [42]. Another possible visual bias includes a preference of the lateral fusiform cortex for foveal rather than peripheral stimuli [43], because words are read in the center of the visual field. However, the metamodal nature of the VWFA, demonstrated here, runs counter to any such purely visual-based hypotheses.

Another possibility is that the VWFA performs a general language function [44]. However, we found a highly significant preference for Braille words over VG (relative to their controls; Figure 2D) in the VWFA in the blind. Furthermore, the tight and reproducible anatomical localization of the VWFA during Braille reading (group general linear model, Figures 1B and 1C; probabilistic map, Figure 2A; single subjects' peaks, Figure 2B) is in contrast with the widespread activation found for language-related tasks in the blind's visual cortex [20, 38]. This pattern rather suggests a robust and specific involvement of the VWFA in reading.

A third explanation is that the VWFA binds "simple features into more elaborate shape descriptions" [45] and then links these descriptions to higher-order stimulus properties such as their associated sound and meaning. This might be accomplished thanks to its particularly direct connection to perisylvian language areas compared to other parts of the ventral visual stream [46]. This view is the most compatible with our results after some adaptation to the metamodal framework: in the case of Braille readers, this function would not be exclusively limited to vision but could also include the tactile modality. This is in line with the more general claim of the distributed domain-specific hypothesis [26, 47, 48], according to which domain-specific organization within a given region is determined not only by the characteristics of its processing but also by the spatial pattern of anatomical and functional connectivity. Such connectivity determines how information in that region relates to salient information that is computed elsewhere. In our case, despite the integration of sensory information from the tactile rather than visual modality, the functional connectivity of the VWFA to language areas still dictates development toward processing the same object domain (reading). However, the VWFA does not necessarily extract information from words in a classical bottom-up manner. An alternative possibility, which also relies on its connections to both sensory and language areas, is that it predicts the tactile or visual form of stimuli that have linguistic content, as described above. Such predictions would benefit from the proximity of the VWFA to language areas, which would generate top-down priors on the basis of semantic knowledge [28].

In conclusion, we propose that the VWFA is a multisensory integration area that possibly binds simple features into more elaborate shape descriptions. Its specific anatomical location and its strong connectivity to language areas enable it to bridge high-level perceptual word representation and language-related components of reading. It is therefore the most suitable region to be taken over during reading acquisition, even when reading is acquired via touch without prior visual experience.

Supplemental Information

Supplemental Information includes one table and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.01.040.

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References

1. McCandliss, B.D., Cohen, L., and Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. Trends Cogn. Sci. (Regul. Ed.) *7*, 293–299.
2. Shaywitz, S.E., and Shaywitz, B.A. (2008). Paying attention to reading: The neurobiology of reading and dyslexia. Dev. Psychopathol. *20*, 1329–1349.
3. Dehaene, S., Pegado, F., Braga, L.W., Ventura, P., Nunes Filho, G., Jobert, A., Dehaene-Lambertz, G., Kolinsky, R., Morais, J., and Cohen, L. (2010). How learning to read changes the cortical networks for vision and language. Science *330*, 1359–1364.
4. Bolger, D.J., Perfetti, C.A., and Schneider, W. (2005). Cross-cultural effect on the brain revisited: Universal structures plus writing system variation. Hum. Brain Mapp. *25*, 92–104.
5. Qiao, E., Vinckier, F., Szwed, M., Naccache, L., Valabrègue, R., Dehaene, S., and Cohen, L. (2010). Unconsciously deciphering handwriting: Subliminal invariance for handwritten words in the visual word form area. Neuroimage *49*, 1786–1799.
6. Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaud, S., and Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the visual word form area. Brain *125*, 1054–1069.
7. Noppeney, U. (2007). The effects of visual deprivation on functional and structural organization of the human brain. Neurosci. Biobehav. Rev. *31*, 1169–1180.
8. Amedi, A., Merabet, L.B., Bermpohl, F., and Pascual-Leone, A. (2005). The occipital cortex in the blind: Lessons about plasticity and vision. Curr. Dir. Psychol. Sci. *14*, 306–311.
9. Pascual-Leone, A., and Hamilton, R. (2001). The metamodal organization of the brain. Prog. Brain Res. *134*, 427–445.
10. Amedi, A., Raz, N., Azulay, H., Malach, R., and Zohary, E. (2010). Cortical activity during tactile exploration of objects in blind and sighted humans. Restor. Neurol. Neurosci. *28*, 143–156.
11. Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.A., and Michel, F. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain *123*, 291–307.
12. Talairach, J., and Tournoux, P. (1988). Co-Planar Stereotaxic Atlas of the Human Brain (New York: Thieme).
13. Sadato, N., Pascual-Leone, A., Grafman, J., Ibañez, 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.
14. Cohen, L.G., Celnik, P., Pascual-Leone, A., Corwell, B., Falz, L., Dambrosia, J., Honda, M., Sadato, N., Gerloff, C., Catalá, M.D., and Hallett, M. (1997). Functional relevance of cross-modal plasticity in blind humans. Nature *389*, 180–183.
15. Büchel, C., Price, C., and Friston, K. (1998). A multimodal language region in the ventral visual pathway. Nature *394*, 274–277.
16. Cohen, L., Jobert, A., Le Bihan, D., and Dehaene, S. (2004). Distinct unimodal and multimodal regions for word processing in the left temporal cortex. Neuroimage *23*, 1256–1270.
17. MacKay, D.J.C. (2003). Information Theory, Inference, and Learning Algorithms (Cambridge: Cambridge University Press).
18. Hair, J.F., Tatham, R.L., Anderson, R.E., and Black, W. (1998). Multivariate Data Analysis, Fifth Edition (New York: Prentiss Hall).
19. Noppeney, U., Friston, K.J., and Price, C.J. (2003). Effects of visual deprivation on the organization of the semantic system. Brain *126*, 1620–1627.
20. Burton, H., Diamond, J.B., and McDermott, K.B. (2003). Dissociating cortical regions activated by semantic and phonological tasks: A FMRI study in blind and sighted people. J. Neurophysiol. *90*, 1965–1982.
21. Calvert, G.A., and Thesen, T. (2004). Multisensory integration: Methodological approaches and emerging principles in the human brain. J. Physiol. Paris *98*, 191–205.
22. Amedi, A., Malach, R., Hendler, T., Peled, S., and Zohary, E. (2001). Visuo-haptic object-related activation in the ventral visual pathway. Nat. Neurosci. *4*, 324–330.
23. Lacey, S., Tal, N., Amedi, A., and Sathian, K. (2009). A putative model of multisensory object representation. Brain Topogr. *21*, 269–274.
24. James, T.W., James, K.H., Humphrey, G.K., and Goodale, M.A. (2006). Do visual and tactile object representations share the same neural substrate? In Touch and Blindness: Psychology and Neuroscience, M.A. Heller and S. Ballesteros, eds. (Mahwah, NJ: Lawrence Erlbaum Associates), pp. 139–155.
25. Renier, L.A., Anurova, I., De Volder, A.G., Carlson, S., VanMeter, J., and Rauschecker, J.P. (2010). Preserved functional specialization for spatial processing in the middle occipital gyrus of the early blind. Neuron *68*, 138–148.
26. Mahon, B.Z., Anzellotti, S., Schwarzbach, J., Zampini, M., and Caramazza, A. (2009). Category-specific organization in the human brain does not require visual experience. Neuron *63*, 397–405.
27. Ma, W.J., and Pouget, A. (2008). Linking neurons to behavior in multisensory perception: A computational review. Brain Res. *1242*, 4–12.
28. Friston, K. (2003). Learning and inference in the brain. Neural Netw. *16*, 1325–1352.
29. Egner, T., Monti, J.M., and Summerfield, C. (2010). Expectation and surprise determine neural population responses in the ventral visual stream. J. Neurosci. *30*, 16601–16608.
30. Burton, H. (2003). Visual cortex activity in early and late blind people. J. Neurosci. *23*, 4005–4011.
31. Moore, C.J., and Price, C.J. (1999). Three distinct ventral occipitotemporal regions for reading and object naming. Neuroimage *10*, 181–192.
32. Vinckier, F., Dehaene, S., Jobert, A., Dubus, J.P., Sigman, M., and Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: Dissecting the inner organization of the visual word-form system. Neuron *55*, 143–156.
33. Binder, J.R., Medler, D.A., Westbury, C.F., Liebenthal, E., and Buchanan, L. (2006). Tuning of the human left fusiform gyrus to sublexical orthographic structure. Neuroimage *33*, 739–748.
34. Bronchti, G., Heil, P., Sadka, R., Hess, A., Scheich, H., and Wollberg, Z. (2002). Auditory activation of "visual" cortical areas in the blind mole rat (Spalax ehrenbergi). Eur. J. Neurosci. *16*, 311–329.

35. Kayser, C., and Logothetis, N.K. (2007). Do early sensory cortices integrate cross-modal information? Brain Struct. Funct. *212*, 121–132.
36. Fujii, T., Tanabe, H.C., Kochiyama, T., and Sadato, N. (2009). An investigation of cross-modal plasticity of effective connectivity in the blind by dynamic causal modeling of functional MRI data. Neurosci. Res. *65*, 175–186.
37. Bavelier, D., and Neville, H.J. (2002). Cross-modal plasticity: Where and how? Nat. Rev. Neurosci. *3*, 443–452.
38. Pascual-Leone, A., Amedi, A., Fregni, F., and Merabet, L.B. (2005). The plastic human brain cortex. Annu. Rev. Neurosci. *28*, 377–401.
39. Deshpande, G., Hu, X., Stilla, R., and Sathian, K. (2008). Effective connectivity during haptic perception: A study using Granger causality analysis of functional magnetic resonance imaging data. Neuroimage *40*, 1807–1814.
40. Salin, P.A., and Bullier, J. (1995). Corticocortical connections in the visual system: Structure and function. Physiol. Rev. *75*, 107–154.
41. Felleman, D.J., and Van Essen, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. Cereb. Cortex *1*, 1–47.
42. Szwed, M., Cohen, L., Qiao, E., and Dehaene, S. (2009). The role of invariant line junctions in object and visual word recognition. Vision Res. *49*, 718–725.
43. Hasson, U., Levy, I., Behrmann, M., Hendler, T., and Malach, R. (2002). Eccentricity bias as an organizing principle for human high-order object areas. Neuron *34*, 479–490.
44. Price, C.J., and Devlin, J.T. (2003). The myth of the visual word form area. Neuroimage *19*, 473–481.
45. Starrfelt, R., and Gerlach, C. (2007). The visual what for area: Words and pictures in the left fusiform gyrus. Neuroimage *35*, 334–342.
46. van der Mark, S., Klaver, P., Bucher, K., Maurer, U., Schulz, E., Brem, S., Martin, E., and Brandeis, D. (2011). The left occipitotemporal system in reading: Disruption of focal fMRI connectivity to left inferior frontal and inferior parietal language areas in children with dyslexia. Neuroimage *54*, 2426–2436.
47. Mahon, B.Z., and Caramazza, A. (2009). Concepts and categories: A cognitive neuropsychological perspective. Annu. Rev. Psychol. *60*, 27–51.
48. Peelen, M.V., and Caramazza, A. (2010). What body parts reveal about the organization of the brain. Neuron *68*, 331–333.
49. Friston, K.J., Holmes, A.P., Price, C.J., Büchel, C., and Worsley, K.J. (1999). Multisubject fMRI studies and conjunction analyses. Neuroimage *10*, 385–396.