

Vision: The Versatile ‘Visual’ Cortex

Dispatch

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The primary visual cortex is, of course, for vision — or so you would think. But it seems that, in blind people, the primary visual cortex can take on an important role in language processing. This suggests considerable flexibility in the processes by which subregions of the human brain become specialised for different functions.

The organisation of the human brain shows a great deal of consistency across individuals. For example, the primary visual cortex (area V1) occupies the calcarine sulcus and occipital pole of the occipital lobe, and there is no question that this is a pivotal region in vision: most visual information ultimately reaching the rest of visual cortex is first funnelled through V1 [1]; functional neuroimaging experiments consistently show activation of V1 by visual stimulation [2]; and visual impairment may be consistently elicited by temporary disruption of neural activity in V1, using transcranial magnetic stimulation (TMS) [3]. Does this mean that the functions of V1 are predetermined from birth? A recent study by Amedi *et al.* [4] shows that the answer is no. Far from lying dormant in blind people, it appears that V1 can take on an important role in high-level linguistic processing. These results suggest a remarkable degree of plasticity in the developing human brain.

Because as much as 35% of the human cortex is typically devoted to vision, early blindness results in the removal of input to a huge expanse of cortical tissue. Previous studies have provided evidence for functional reorganisation as a consequence. For instance, in blind participants (but not sighted control participants) V1 is involved in processing tactile input during Braille reading [5]. A recent functional magnetic resonance imaging (fMRI) study suggested that, in blind participants, V1 is involved in linguistic processing, regardless of the sensory modality of input (tactile or auditory) [6].

An important shortcoming of functional neuroimaging studies, however, is that although they can establish that a brain region becomes activated when participants perform a certain task, they cannot show that this brain region is necessary for performance of the task. For example, if participants were to perform an extremely easy, monotonous task during an fMRI scan, the ‘boredom centres’ of their brains might become highly active. But this does not mean that these boredom centres are actually functionally involved in allowing them to perform the task.

In the study by Amedi *et al.* [4], a group of blind participants — all of whom became blind before the

age of four — and a control group of sighted participants performed a language production task in which they heard a series of nouns. In response to these nouns, participants were required to generate an appropriate verb as quickly as possible. For instance, given the word ‘apple’, an appropriate response might be to say ‘eat’ (Figure 1A). Immediately after the end of noun presentation, a train of TMS pulses was delivered to a specific cortical site (Figure 1B), creating a temporary virtual lesion [7]. In this way, the investigators were able to compare the effects of disrupting activity in various cortical regions on language processing.

In both sighted and blind participants, TMS over the left inferior prefrontal cortex (PF) was associated with a greater error rate in the task, in comparison with stimulation of a control site (somatosensory cortex) or a sham TMS control condition that did not disrupt cortical activity. This result is in good agreement with previous studies implicating PF in language processing [8]. But whereas stimulation of V1 had no adverse effect on the performance of sighted participants, it caused significant impairment in the performance of blind participants. This reduction in performance was largely caused by an increased rate of semantic errors — saying a completely unrelated word in response to the noun — rather than problems with the sensory or motor components of the task. Indeed, participants reported that their errors were mostly in ‘coming up with the right word’, rather than being caused by difficulty in hearing and understanding the nouns correctly, or in moving their lips or tongue to form the verb in reply. Thus, the results show that V1, an area involved in analysing visual input in sighted participants, plays a functional role in semantic aspects of language processing in blind people.

It is now well established that primary sensory areas which are usually dedicated to one sensory modality can become responsive to a different modality if their inputs are switched at birth [9]. What is remarkable about the findings of Amedi *et al.* [4] is that they suggest that, not only can V1 take on a non-visual function in blind people, but it can also take on a high-level non-sensory function. How does a primary sensory area come to be involved in language processing? One possibility is that V1 first becomes specialised for processing tactile input during Braille-reading [5], which then provides a stepping stone into higher-level language processing.

A general principle of functional organisation in the human cortex is that representations become increasingly abstract as one moves in an anterior direction [10,11]. The results of Amedi *et al.* [4] show that the developing human brain need not follow this principle if it is deprived of visual input. This points to considerable plasticity in human cortical development. It seems reasonable to speculate that we are born with a ‘primary visual cortex’ which is up for grabs. If it is not recruited for the processing of visual input, other functions will fill the vacuum, perhaps explaining the superior talents of blind people in certain non-visual domains [6,12]. This

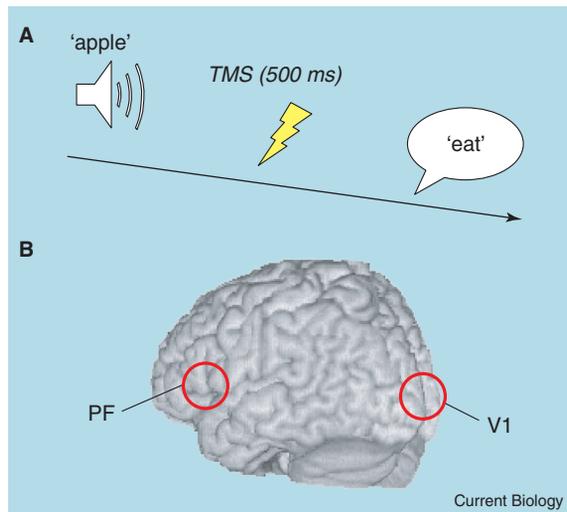


Figure 1.
(A) The task used by Amedi *et al.* [4]. Immediately after the presentation of a noun, repetitive TMS was delivered for 500 ms, after which the participant responded with a semantically related verb. (B) Two sites of transcranial magnetic stimulation. TMS over left inferior prefrontal cortex (PF) was associated with an increased error rate in both sighted and blind participants. By contrast, stimulation of primary visual cortex (V1) increased the number of errors only in blind participants.

tallies with recent theoretical accounts that conceive of functional specialisation in the human cortex as being the product of dynamic interplay between genetic and environmental factors during development, rather than being predetermined at birth [13].

A question, which has clear implications for neurorehabilitation, is whether the plasticity demonstrated by this study is also present in the adult brain following changes later in life than in the subjects of Amedi *et al.* [4]. Does the brain always retain an ability to reorganise its functions, or is there a 'point of no return', after which neurons become too set in their ways to take on a new role? All of the blind participants investigated by Amedi *et al.* [4] became blind before the age of four (and most had been blind since birth). However, functional neuroimaging studies have suggested that the visual cortex of people who become blind later in life may also undergo reorganisation, though perhaps to a less radical degree [14]. Thus an important topic for future research will be to investigate the decline of plasticity with age, and what can be done to overcome this.

References

1. Felleman, D.J., and Van Essen, D.C. (1991). Distributed hierarchical processing in primate cerebral cortex. *Cerebr. Cortex* 1, 1-47.
2. Tootell, R.B.H., Hadjikhani, N.K., Vanduffel, W., Liu, A.K., Mendola, J.D., Sereno, M.I., and Dale, A.M. (1998). Functional analysis of primary visual cortex (V1) in humans. *Proc. Natl. Acad. Sci. USA* 95, 811-817.
3. Amassian, V.E., Cracco, R.Q., Maccabee, P.J., Cracco, J.B., Rudell, A.P., and Eberle, L. (1998). Transcranial magnetic stimulation in study of the visual pathway. *J. Clin. Neurophysiol.* 15, 288-304.
4. Amedi, A., Floel, A., Knecht, S., Zohary, E., and Cohen, L.G. (2004). Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. *Nat Neurosci.* 7, 1266-1270.
5. Cohen, L.G., Celnik, P., Pascual-Leone, A., Corwell, B., Faiz, 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* 1997, 389, 180-183.
6. Amedi, A., Raz, N., Pianka, P., Malach, R., Zohary, E. (2003). Early 'visual' cortex activation correlates with superior verbal-memory performance in the blind. *Nat. Neurosci.* 6, 758-766.
7. Walsh, V., and Pascual-Leone, A. (2003). *Transcranial Magnetic Stimulation: A Neurochronometrics of Mind*: MIT Press.
8. Gabrieli, J.D.E., Poldrack, R.A., and Desmond, J.E. (1998). The role of left prefrontal cortex in language and memory. *Proc. Natl. Acad. Sci. USA* 95, 906-913.
9. Sur, M., and Leamey, C.A. (2001). Development and plasticity of cortical areas and networks. *Nat. Rev. Neurosci.* 2, 251-262.
10. Ungerleider, L.G., and Haxby, J.V. (1994). 'What' and 'Where' in the human brain. *Curr. Opin. Neurobiol.* 4, 157-165.
11. Koechlin, E., Ody, C., and Kouneiher, F. (2003). The architecture of cognitive control in the human prefrontal cortex. *Science* 302, 1181-1185.
12. Gougoux, F., Lepore, F., Lassonde, M., Voss, P., Zatorre, R.J., and Belin P. (2004). Pitch discrimination in the early blind. *Nature* 430, 309.
13. Elman, J.L., Bates, E.A., Johnson, M.H., Karmiloff-Smith, A., Parisi, D., and Plunkett, K. (1996). *Rethinking Innateness: A Connectionist Perspective on Development*: MIT Press.
14. Burton, H. (2003). Visual cortex activity in early and late blind people. *J. Neurosci.* 23, 4005-4011.