Evolution of human cortical circuits

for reading and arithmetic:

The "neuronal recycling" hypothesis.

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Introduction

Humans have a remarkable ability to invent symbols systems such as Arabic numerals or the alphabet. This capacity is unique in the animal kingdom. Thus, one has to ask what is so special about the human brain that allows it to expand its functionality by acquiring new cultural tools.

A first possibility is that, relative to other animals, the human brain has evolved new specialized processors, each providing access to a new cognitive function. For instance, our species may have evolved some special brain mechanisms for recursion that would give us access to the domain of syntax (Hauser, Chomsky, & Fitch, 2002). However, such a possibility is excluded for recent cultural acquisitions such as reading or arithmetic. Those activities are far too recent to have exerted any evolutionary pressure on brain evolution. Reading, for instance, was invented only 5400 years ago, and symbolic arithmetic is even more recent: the Arabic notation and most of its associated algorithms were not available even a thousand year ago. Thus, it is logically impossible that there exist dedicated brain mechanisms evolved for reading or symbolic arithmetic.

An alternative theory is that those capacities rely upon an extended range of cortical plasticity unique to humans. According to this second hypothesis, the human brain would be special in its capacity to accommodate a broad range of new functions through learning. At one extreme, it may be suggested that the architecture of our brain exerts little or no constraints on the range of competences that we can acquire, because we are equipped with broad if not universal mechanisms of learning. Although admittedly presented here in somewhat caricatured form, this view is not so distant from some modern connectionist or neo-constructivist statements (e.g. Quartz & Sejnowski, 1997). While such a learning-based theory might explain the vast range of human cultural abilities, it implies that the brain implementation of those abilities should be highly variable across individuals. Depending on

an individual's learning history, the same brain region might become involved in various functions. During learning, random symmetry breaking might ultimately lead to the assignment of dedicated territories to different competences, but this assignment should be randomly determined for different individuals. Thus, one would not expect to find reproducible cerebral substrates for recent cultural activities such as reading and arithmetic.

The purpose of the present chapter is to examine where the data stand. A wealth of recent neuroimaging and neuropsychological findings shed light on the ability of the human brain to acquire novel cultural objects such as reading and arithmetic. As we shall see, those data go against the hypothesis of an unbiased, random symmetry-breaking theory of cultural learning. Converging psychological, neuropsychological and brain-imaging evidence demonstrates that the adult human brain houses dedicated mechanisms for reading and arithmetic. Small cortical regions, which occupy reproducible locations in different individuals, are recruited by these tasks. They accomplish their function automatically and often without awareness. Furthermore, the lesion of those regions can lead to specific reading or calculation impairments. In brief, the evidence seems to support the existence of distinct, reproducible and rather specific brain bases for reading and arithmetic.

The paradox, of course, is that given the available evolutionary time, it is impossible that the architecture of our brains has somehow adapted to the specific problems posed by these cultural tools. Closer examination of the function of the relevant brain areas, however, suggests a possible resolution of this paradox. It is not the case that those areas acquire an entirely distinct, culturally arbitrary new function. Rather, they appear to possess, in other primates, a prior function closely related to the one that they will eventually have in humans. Furthermore, many of the functional features that make them highly efficient in processing human cultural tools are already present. Thus, relatively small changes may suffice to adapt them to their new cultural domain.

I conclude the paper by tentatively proposing the "neuronal recycling" hypothesis: the human capacity for cultural learning relies on a process of pre-empting or recycling pre-existing brain circuitry. According to this third view, the architecture of the human brain is limited and shares many traits with other non-human primates. It is laid down under tight genetic constraints, yet with a fringe of variability. I postulate that cultural acquisitions are only possible insofar as they fit within this fringe, by reconverting pre-existing cerebral predispositions for another use. Accordingly, cultural plasticity is not unlimited, and all cultural inventions should be based on the pre-emption of pre-existing evolutionary adaptations of the human brain. It thus becomes important to consider what may be the evolutionary precursors of reading and arithmetic.

Cerebral bases of arithmetic

Calculation and the human intraparietal sulcus

Convergent imaging and neuropsychological results associate mental arithmetic with the parietal lobe (Dehaene, Piazza, Pinel, & Cohen, 2003). The left and right intraparietal regions are systematically activated whenever subjects engage in calculation (Chochon, Cohen, van de Moortele, & Dehaene, 1999; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Gruber, Indefrey, Steinmetz, & Kleinschmidt, 2001; Lee, 2000; Pesenti, Thioux, Seron, & De Volder, 2000; Rickard et al., 2000; O. Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002; Zago et al., 2001). Their degree of activation is directly proportional to the difficulty of the arithmetic task, as measured by the size of the numbers involved, the numerical distance that separates them, or the number of operations to be performed in a given time (Menon, Rivera, White, Glover, & Reiss, 2000; Pinel, Dehaene, Riviere, & LeBihan, 2001; Stanescu-Cosson et al., 2000).

The interpretations of these findings, however, remains debated. According to one theory, a bilateral subregion of the parietal lobe, located deep inside the intraparietal sulcus, contains a domain-specific representation of numerical quantity (Dehaene & Cohen, 1995; Dehaene, Piazza et al., 2003). An alternative "domain-general" view, however, proposes that no cortical sector is dedicated to number processing (T. Simon, 1999), and that the engagement of the parietal lobe during calculation can be explained entirely by concomitant task components such as finger counting and visuo-spatial working memory (Gruber et al., 2001; Zago et al., 2001).

Several findings support the domain-specific hypothesis. First, when multiple visuo-spatial, language and calculation tasks are imaged in the same subjects, a small subregion in the depth of the horizontal segment of the intraparietal sulcus (hereafter called the HIPS region), is found active solely during calculation (O. Simon et al., 2002). Thus, its activation cannot be reduced to spatial, attentional, eye or finger movement artifacts. Second, the HIPS activates when subjects merely have to detect Arabic numerals, but not letters or colors, in a stream of auditory or visual stimuli (Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003). This indicates that neither calculation nor working memory are needed to obtain parietal number-related activations. Indeed, the HIPS is even activated by subliminal numerals, indicating automatic access to quantity information from number symbols (Naccache & Dehaene, 2001). Third, a recent meta-analysis (Dehaene, Piazza et al., 2003) indicates that the HIPS is jointly activated by essentially all number processing contrasts that have been used in the literature, and particularly when the task puts emphasis on quantity processing (figure 1). It is unlikely that all experiments are affected by identical artifacts, especially considering that some studies have contrasted highly similar tasks with the same difficulty level as measured by response time and error rate (e.g. approximation relative to exact calculation: Dehaene et al., 1999).

Further evidence for the tight relation between the HIPS and mental arithmetic comes from the classical neuropsychological finding that lesions to the left parietal cortex cause severe impairments in calculation, sometimes without much concomitant cognitive impairment in other domains of reasoning (e.g. Dehaene & Cohen, 1997; Lee, 2000; Takayama, Sugishita, Akiguchi, & Kimura, 1994). Brain imaging and neuropsychological evidence point to even more selective dissociations, for instance, between subterritories for subtraction and multiplication (Duffau et al., 2002; Lee, 2000).

Precursors of arithmetic in animals

In the last decades, the systematic investigation of precursors of numerical abilities in animals has shed some light on the biological origins of human arithmetic. Behavioral investigations have revealed that animals such as rats, pigeons, or monkeys can extract the approximate numerosity of auditory or visual sets of objects (see e.g. Brannon, this volume; Nieder & Miller, this volume). Numerosity is represented by animals independently of other parameters such as object size or shape (Brannon & Terrace, 1998). Evidence from wild animals indicates that numerosity is part of the spontaneous representational repertoire of many animal species, and does not need to be inculcated by training (Hauser, Carey, & Hauser, 2000; Hauser, Dehaene, Dehaene-Lambertz, & Patalano, 2002; McComb, Packer, & Pusey, 1994). Even when training is involved in laboratory animals, experiments have demonstrated generalization patterns that goes beyond what the animals could have acquired by mere stimulus-driven learning. For instance, macaques trained to order the numerosities 1 though 4 generalized spontaneously to the range of numbers 5 through 10 (Brannon & Terrace, 1998). Likewise, macaques trained on a matching-to-sample task with training stimuli where number and total size were confounded later generalized on the basis of number, not total size when the two parameters were unconfounded (Nieder, Freedman, & Miller, 2002). Finally, there is some evidence that animals can use these number

representations for simple approximate calculations such as addition or subtraction (e.g. Hauser et al., 2000).

Crucial to the link between animal research and human neuroimaging studies of arithmetic is the recent finding of a neurobiological substrate for animal number processing. In agreement with the predictions of a neural network model (Dehaene & Changeux, 1993), neurons tuned to numerosity were recently recorded in macaque monkeys trained to perform numerosity-dependent motor or matching tasks (Nieder et al., 2002; Nieder & Miller, 2003; Nieder &Miller, this volume; Sawamura, Shima, & Tanji, 2002). One such neuron might respond to visual displays of 3 objects, regardless of their spatial organization, size or shape, while responding much less to 2 or 4 objects and not at all to one object or to five objects. Crucially, such neurons are found in dorsolateral prefrontal cortex, but also in the vicinity of the intraparietal sulcus, with the latest evidence suggesting a precise localization in the depth of the middle portion of the IPS, possibly within area VIP (Nieder & Miller, this volume). As demonstrated in figure 1, this localization in macaques constitutes a plausible homolog of the human site of activation during symbolic arithmetic tasks. It was indeed predicted on the basis of the localization of human arithmetic-related activations relative to putative human homologs of parietal areas LIP and AIP (O. Simon et al., 2002).

A similar principle of numerosity tuning in monkeys and humans

In order to demonstrate that the monkey competence for approximate numerosity representation is a plausible precursor of human arithmetic, one should ideally show that the human HIPS region also contains numerosity-sensitive neurons. Yet most human neuroimaging studies have used symbolic stimuli (e.g. Arabic digits) and have not probed basic numerosity processing. Furthermore, single neurons are not accessible in humans with non-invasive methods. Recently, however, my colleagues and I have used an habituation

design to demonstrate numerosity tuning in the human HIPS (Piazza, Izard, Pinel, Le Bihan, & Dehaene, submitted).

We recorded whole-brain fMRI images continuously while subjects were repeatedly presented with many visual displays of a fixed, large numerosity (e.g. always 16 dots). We reasoned that this should lead to habituation of a coarse population of numerosity detectors tuned around the numerosity 16. We then "read-out" this on-going state of habituation by recording the event-related fMRI activation to a single deviant numerosity (ranging from 8 to 32 dots). As predicted, the only regions that responded to numerosity change were the left and right intraparietal sulci, at the precise location of the HIPS. Activation in those regions followed an inverse Gaussian function centered around the habituated numerosity (figure 2): it was low for deviant numerosities that fell close to the habituation numerosity (e.g. 16 followed by 20), but increased on either side as the deviant numerosity became more distant (e.g. 16 followed by 8 or by 32). This experimental design allowed us to indirectly trace the average tuning curve of the underlying neural population. The details of this fMRI tuning function were identical to those observed in the monkey: (a) Tuning was independent of the presence or absence of a concomitant change in object shape; (b) Tuning width doubled when the habituation numerosity doubled, indicating that the representation of numerosity follows Weber's law: the precision of the representation decreases linearly with the size of the numbers involved; (c) As in single-cell data, the measured responses were best described by a Gaussian tuning curve with a fixed width on a logarithmic number line.

Learning to map Arabic and verbal symbols onto the quantity code

The presence of an evolutionary precursor of arithmetic in animals helps resolve the paradox described in the introduction, by demonstrating that arithmetic is not, after all, a completely arbitrary cultural invention. Although the particular symbols and algorithms that we use are conventional, our very ability to invent them rests on an intuitive understanding or

"core knowledge" of the number domain, which has been termed "number sense" (Dehaene, 1997). My hypothesis is that the human acquisition of Arabic numerals and arithmetic is possible, and occurs with a reproducible underlying brain substrate, because human children learn to connect their pre-existing intraparietal representation of numerosity with the new arbitrary words and symbols that they are taught. During symbolic calculation, humans quickly access this quantity representation, and they rely on its approximate numerosity code for operations of comparison and approximate calculation. Thus, an evolutionarily ancient representation is put to use for culturally novel symbolic manipulations, including elaborate mathematical ones.[1]

The hypothesis of a reliance on the animal numerosity representation during human symbolic operations makes several predictions, many of which have been verified. First, human adults, even during symbolic task with Arabic numerals, should show evidence of analog magnitude processing. Indeed, continuous distance effects and Weber's law are characteristically observed in both human and animals in a broad variety of symbolic and non-symbolic tasks (Barth, Kanwisher, & Spelke, 2003; Cordes, Gelman, Gallistel, & Whalen, 2001; Pinel et al., 2001; Whalen, Gallistel, & Gelman, 1999). This holds even when such effects are deleterious to performance (e.g. when being slower to compare 59 with 65

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[1] Before we reach a complete theory of number-word acquisition, two issues will have to be clarified through further experimentation. First, there is evidence that another system of "object tracking", able to encode up to three objects, contributes to some but not all numerical tasks in addition to the analog magnitude system. This tracking system is present early on in infancy (Feigenson, Carey, & Hauser, 2002) and exists in other primates (Hauser et al., 2000). Its neural bases is currently unknown (though see Piazza, Giacomini, Le Bihan, & Dehaene, 2003; Sathian et al., 1999), as is the exact nature of its contribution to linking symbols and quantities. Second, the human analog quantity representation is probably not passively linked to number symbols, but may be significantly modified in the process – at least in its precision (Weber fraction), but possibly more deeply, for instance in its representation of large numbers and of base 10.

than 51 with 65, although focusing on the leftmost digit would seem sufficient to decide that both are smaller) (Dehaene & Akhavein, 1995; Dehaene, Dupoux, & Mehler, 1990). In fMRI, distance-dependent numerical priming, conceptually similar to the above numerosity-dependent habituation, has been obtained with masked Arabic and verbal numerals, suggesting that this region is coding jointly for numbers presented in symbolic and non-symbolic form (Naccache & Dehaene, 2001).

A second consequence is that human infants, prior to schooling or even to language acquisition, should exhibit a primitive "number sense" comparable to animals. Indeed, behavioral evidence indicates that infants in the first year of life can process numbers. Although there is some debate about the origins of this competence (Feigenson et al., 2002), it arises at least in part from an analog magnitude system similar to the monkey's, capable of dealing with relatively large approximate numerosities (e.g. 8 versus 16) and obeying Weber's law (Brannon, 2002; Xu, 2003; Xu & Spelke, 2000).

Third, early lesions of the HIPS should severely interfere with the development of arithmetic. Indeed, recent neuroimaging studies of children suffering from developmental dyscalculia have revealed demonstrable intraparietal insults that can sometimes be dated to prenatal or perinatal injuries (Isaacs, Edmonds, Lucas, & Gadian, 2001; L. M. Levy, Reis, & Grafman, 1999). My colleagues and I recently showed that a genetic disease, Turner's syndrome, is associated with behavioral, neuro-anatomic, and functional activation impairments associated with the intraparietal sulcus (Molko et al., 2003). The existence of such selective impairments in other normally intelligent children supports the view that arithmetic does not emerge solely from a cultural construction process, but requires the integrity of specific brain structures that provide a conceptual foundation for learning.

Cerebral bases of reading

The visual word form area

I now turn to the cerebral bases of another important human cultural invention: reading. Reading even a single word activates a distributed set of brain regions (Fiez & Petersen, 1998), many of which are shared with spoken language processing. Here, however, I concentrate on one activation site, located in the left occipito-temporal sulcus. There is evidence that this region, which has been termed the "visual word form area" (VWFA), is highly attuned to words in the subject's acquired script. This presents an apparent paradox parallel to the one raised by studies of calculation, inasmuch as there has not been any evolutionary time to evolve a brain area dedicated to reading.

The VWFA is easily identified by collecting fMRI data during short presentations of written words, under passive viewing instructions as well as during active tasks such as semantic classification. Activation is systematically observed in the left occipito-temporal sulcus on the lateral border of the fusiform gyrus (figure 3A), whether words are contrasted with a fixation control (Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002) or with presentation of more controlled visual stimuli such as checkerboards (Cohen et al., 2002), pictures of faces, textures, or buildings (Gauthier et al., 2000; Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Puce, Allison, Asgari, Gore, & McCarthy, 1996), pseudo-letters or even random consonant strings (Cohen et al., 2002; Price, Wise, & Frackowiak, 1996). The VWFA can be identified in any single subject (Cohen et al., 2000; Cohen et al., 2002; Dehaene et al., 2002; Gauthier et al., 2000; Puce et al., 1996), allowing quantification of its spatial variability, which appears remarkably low. The standard deviation of its peak coordinates in the Talairach system is about 5 millimeters (Cohen et al., 2000; Dehaene et al., 2002). Furthermore, it occupies a systematically more lateral location relative to the fusiform

activation induced by faces (Puce et al., 1996), and falls at a systematic location relative to larger-scale maps of retinotopic and object preference (Hasson et al., 2002).

This reproducible localization is incompatible with many connectionist models of learning to read. Polk and Farah (1998), for instance, presented a model in which distinct regions for numbers and letters emerged through Hebbian learning within an initially unbiased visual layer. In their model, neurons dedicated to letters emerged at a random location and then grouped together to form local letter-sensitive patches. The neuroimaging data suggest that this view cannot be correct. The sites of visual activation during reading are both restricted and highly reproducible, suggesting that there is considerable bias in the underlying cortical tissue prior to learning to read.

Evidence for functional specialization and cultural impregnation

Three pieces of evidence indicate that the VWFA is functionally specialized for extracting an abstract, invariant representation of letters strings. First, it only activates for visual, not for spoken words (unless the task induces top-down processing; for discussion, see Cohen & Dehaene, 2003). Furthemore, its lesioning leads to pure alexia, a deficit of visual but not spoken word recognition. Indeed, there is good anatomical convergence between the activation site during reading in normal subjects, and the common lesion site in pure alexia (see figure 3A; Cohen et al., in press). Second, the VWFA is activated by both real words and pronounceable pseudo-words, more than by consonant strings (Cohen et al., 2002; Dehaene et al., 2002; Price et al., 1996). This suggests an intervention at a prelexical stage of processing, and also implies that this area has been changed by learning to read. The selection of letters shapes is an arbitrary cultural convention, and the stimuli that we used as consonant strings could have been words in another script. Thus, the stronger response to words than to consonant strings indicates that the VWFA has become attuned to reading in a specific script (Cohen et al., 2002).

Third, the VWFA computes an invariant representation of visual words, one that abstracts away from irrelevant surface variations in the visual stimulus. The VWFA is the first visual area that responds in a non-retinotopic manner, with convergence of activation towards the left hemisphere whether the words are presented left or right of fixation (Cohen et al., 2000). In addition to this spatial invariance, using subliminal priming experiments we demonstrated that the VWFA also computes invariance for upper or lower case (figure 3B). When a visible target word is preceded by a short, subliminal presentation of a masked prime word, both response time and fMRI activation are reduced if the target and prime correspond to the same word (Dehaene et al., 2001). Crucially, the VWFA is the only visual area in which this repetition suppression phenomenon is independent of case: it is identical whether the visual stimuli are presented in the same case (e.g. radio/radio) or in a different case (e.g. radio/RADIO). In a recent replication, I showed that such cross-case priming obtains even for words made of letters that are highly dissimilar in upper and lower case, and for which the pairing of upper and lower case is merely a matter of cultural convention (e.g. A and a; Dehaene, Jobert et al., 2003). Again, this implies that this brain area is very finely attuned to the specific demands of our reading system.

Possible precursor of the visual word form area in monkeys

Altogether, fMRI studies in humans indicate a rather fine functional tuning of a small, reproducible subpart of the visual system to the demands of visual word recognition, including sensitivity to arbitrary cultural conventions such as variations in case. How can such a specialization arise, although the human brain cannot possibly be predisposed for reading? We can shed some light on this issue by consider the function of this area in other primates, or in human prior to learning to read. In humans, the VWFA belongs to the ventral stream for visual recognition. Indeed, even in word-responsive voxels, responses to pictures or drawings of objects can often be elicited (Hasson et al., 2002). fMRI studies comparing the cortical

responses to scrambled versus unscrambled objects in humans and macaques suggest that the higher-level regions of visual ventral cortex in humans may be homologous to the infero-temporal cortex (area IT) of the macaque (Tootell, Tsao, & Vanduffel, 2003). Furthermore, optical and single-unit recordings indicate that IT neurons possess a high degree of visual invariance (Tanifuji, this volume; Ito, Tamura, Fujita, & Tanaka, 1995; Sary, Vogels, & Orban, 1993; Tanaka, 1996). Their receptive fields are vast, often including most or all of the bilateral visual field. They respond preferentially to certain objects, and maintain this preference across a large range of changes in size and retinal location. Some neurons even respond to different views of the same object, for instance the profile and front view of a face, and can learn to respond to arbitrarily related views (Logothetis, 2000; Miyashita, 1988).

These properties suggest that IT neurons are ideally suited to learn to respond to letter, grapheme, and word shapes in a location and case-invariant way. Invariance in visual word recognition may actually result from the intrinsic properties of location and viewpoint invariance found in IT neurons prior to learning to read.

Keiji Tanaka, Manabu Tanifuji and their colleagues have further dissected the selective preferences of IT neurons (see Tanifuji, this volume). They have observed that, when a neuron responds to a complex object such as the head of a cat, it is often possible to identify a simpler shape to which the neuron is optimally responsive (for instance a black disk on a white background, similar to an "eye"). IT cortex seems to be composed of a mosaic of such elementary visual detectors (Tanaka, 1996). It is remarkable that many of those minimal shapes resemble our letters. Some neurons, for instance, fire to two superimposed disks that form a figure of 8, others respond to two bars forming a T, and yet others may respond to an asterisk or a circle. Neurons responsive to these forms may have been selected, during either phylogenesis or ontogenesis, because as an ensemble they provide a repertoire that can

represent an immense variety of object shapes. The T shape, for instance, is useful because it frequently signal occlusion of a contour behind some part of the object.

One may therefore speculate that the capacity of this region to learn letter shapes is not an accident. Rather, it derives from the evolutionary and developmental history of IT cortex as a visual recognition system. The minimal shapes that this area can easily represent have been discovered and exploited in our writing systems. In that hypothesis, it is not the human cortex that has evolved for reading -- there was not enough evolutionary time and pressure for such an evolution. Rather, writing systems themselves evolved under the constraint of having to remain learnable and easily recognizable by our primate visual system.

Finally, how can one explain the precise location of the VWFA, which is reproducible within a few millimetres across different subjects ? There are, in fact, several such examples of precise localization in the visual system. Local preferences for objects, faces, places, and body parts are also fairly reproducible across subjects (Kanwisher, this volume; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). Rafi Malach and his colleagues suggest that those preferences correspond to fixed locations relative to a large-scale gradient of preference for image excentricity. In human inferotemporal cortex, lateral regions respond preferentially to foveal images, while medial regions prefer parafoveal stimuli (Hasson et al., 2002; I. Levy, Hasson, Avidan, Hendler, & Malach, 2001; Malach, Levy, & Hasson, 2002). This gradient of excentricity preference cuts across all visual areas of the ventral stream, and may be laid down early on during cortical development, perhaps under the genetic control of an early diffusive "morphogen" substance (Turing's model of morphogenesis). The presence of such an early bias may explain why visual word recognition, which requires high visual accuracy and hence foveation, is systematically located in the lateral inferotemporal cortex. Its lateralization to the left hemisphere might be further explained, similarly, by the presence of

privileged connections with multiple language areas of the left hemisphere, particularly the temporal and frontal regions involved in speech comprehension and production.

Learning to read changes human infero-temporal cortex

In summary, I speculate that the human brain can learn to read because part of the primate visual ventral object recognition system spontaneously accomplishes operations closely similar to those required in word recognition, and possesses sufficient plasticity to adapt itself to new shapes, including those of letters and words. During the acquisition of reading, part of this system becomes highly specialized for the visual operations underlying location- and case-invariant word recognition. It occupies a reproducible location within the left occipito-temporal sulcus because the neurons at this location possess intrinsic properties of foveal sensitivity, projection to distant areas in the left hemisphere, and perhaps other undiscovered features that render them most suited for this acquisition. Thus, reading acquisition proceeds by selection and local adaptation of a pre-existing neural region, rather than by *de novo* imposition of novel properties onto that region.

In this view, the VWFA should not be considered as a "module" for visual word recognition, but rather as a population of neurons, distributed and overlapping with other populations involved in object recognition, which becomes progressively attuned to the reading process. This view predicts that preference for written words in this region should be relative rather than absolute, and should emerge progressively during learning to read, as the child acquires increasing expertise in word recognition. Indeed, developmental fMRI studies have identified a correlation between VWFA activation and reading skill (B. A. Shaywitz et al., 2002). Furthermore, in dyslexic individuals, this region does not respond normally to letters and words (Paulesu et al., 2000; S. E. Shaywitz et al., 1998). This reduced activation may not be causally related to dyslexia, but rather may reflect a lack of automatization of word recognition resulting from a primary phonological deficit.

General principles of cultural pre-emption

The two examples of cultural activities that I have considered, arithmetic and reading, exhibit significant commonalities, but also differences. In both cases, humans learn to attribute meaning to conventional shapes (Arabic digits or the alphabet), and they eventually do so in a highly efficient manner, even subliminally. Furthermore, the brain activations associated with these cultural activities are highly reproducible. Finally, the brain areas involved turn out to have a significantly related function in primate evolution. There is however an important difference between arithmetic and reading. On the one hand, there is a genuine precursor of number knowledge in primate evolution. Intraparietal cortex already seems to be involved in number representation in primates, and the cultural mapping of number symbols onto this representation significantly enhances, but does not radically modify its computational capacity. On the other hand, the evolutionary precursor of the visual word form area is initially unrelated to reading. It evolved for object recognition, a function significantly different from the mapping of written language onto sound and meaning.

As a generalization of those two examples, I tentatively propose that the human ability to acquire new cultural objects relies on a neuronal "reconversion" or "recycling" process whereby those novel objects invade cortical territories initially devoted to similar or sufficiently close functions[2]. According to this view, our evolutionary history, and therefore

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[2] The Merriam-Webster dictionary defines the verb "to recycle" as "to pass again through a series of changes or treatments" or "to adapt to a new use". The French term « recyclage » has a slightly different meaning, closer to what I intend to convey. The primary meaning of "recyclage" applies to students or employees and refers to a change in their orientation or to a complementary formation period designed to adapt them to a new job (the English equivalent might be "retraining" or "reorientation"). It should be clear that my use of the word "recycling" does not imply that the initial function of a given brain area, prior to cultural acquisition, should be considered as garbage, as one referee suggested! I emphasize that cultural reconversion or "neuronal recycling"

our genetic organization, has created a cerebral architecture that is both constrained and partially plastic, and that delimits a space of learnable cultural objects. New cultural acquisitions are therefore possible only inasmuch as they are able to fit within the pre-existing constraints of our brain architecture.

The present hypothesis bears considerable similarity with a classical Darwinian concept which has been called "tinkering" by François Jacob (1977) or "exaptation" by Gould and Vrba (1982) – the re-utilization, during phylogenesis, of biological mechanisms for a new function different from the one for which they evolved. In the case of cultural objects, however, this process takes place at a shorter time scale of weeks, months or years, through epigenetic mechanisms that do not require any change in the genome. The terms "reconversion" or "recycling" capture the idea that this process occurs in the lifetime of the individual: each cultural acquisition must find its ecological niche in the human brain, a circuit whose initial role is close enough and whose flexibility is sufficient to be reconverted to this new role.

The terms "reconversion" or "recycling" also make clear that the neuronal tissue that supports cultural learning is not a blank slate, but possesses prior properties (though perhaps only in the form of small biases). Not any kind of object can be made of recycled glass or paper: those materials possess intrinsic physical properties that make them more suitable for some uses that for others. Likewise, each cortical region or network possesses intrinsic properties that are adapted to the function it evolved for, and are only partially modifiable during the cultural acquisition process. Cultural learning in humans may never totally overturn such pre-existing biases, but rather changes them minimally as needed. Thus,

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transforms what was initially a useful function in our evolutionary past into another function which is currently more useful within the present cultural context.

cultural objects may not be infinitely malleable, and should in fact often reflect intrinsic constraints of the underlying neural networks.

I end by emphasizing three consequences of this view, and examining how they might apply to reading and arithmetic.

Prediction 1: Our genetic envelope should limit the set of learnable cultural objects. Contrary to the view that learning is an open-ended source of unbounded cultural variation, the recycling hypothesis predicts that the human capacity for cultural invention, although extensive, is eventually limited by the envelope of possibilities inherent in our brain circuits. This should lead to a reanalysis of the extent of cultural diversity. There may be a common structure beyond the obvious cultural variations. Seen in this light, writing systems, for instance, appear as relatively invariable: they all use a small repertoire of highly contrasted, basic, foveal shapes; they all map those shapes onto a mixture of sounds and morphemes; and they all take for granted that character size and location are irrelevant (although this invariance does not need to be explicitly taught). Some of these properties may reflect the evolutionary constraints of the cerebral circuits that are pre-empted when we acquire reading. This view also predicts that there should be unlearnable writing systems. Although this has not been tested, it seems likely that computer bar codes, for instance, in which information is encoded in binary form by fine metric cues, would not be learnable by a human.

Prediction 2: Learning difficulty should depend on the distance between the initial function and the new one. It should possible to account for the difficulty of acquiring a new cultural tool based on the amount of transformation that separates the initial, evolutionarily inherited function of the underlying brain circuits and the new, culturally acquired one. The recycling hypothesis predicts that pre-existing biases should often speed-up the cultural acquisition of novel material. In arithmetic, for instance, the availability of a

preverbal analog representation of number magnitude is thought to facilitate the acquisition of Arabic symbols and the counting sequence, because it provides even very young children with an intuitive grasp of the number domain and its basic principles (Dehaene, 1997; Gelman & Gallistel, 1978). In reading, similarly, the properties of size and location invariance that are intrinsic to the visual system are likely to considerably speed up reading acquisition because they provide a stable visual representation of letters to correlate with phonological representations of word sound. The ease or "transparency" of this mapping may then become a crucial determinant of speed and efficiency of learning to read in different languages (e.g. Paulesu et al., 2001).

More generally, the efficiency of education should be greatly enhanced by using teaching strategies that capitalize upon the pre-existing representations that young children possess prior to entering school. For instance, finger counting, token counting, and the abacus may provide excellent support for early arithmetic learning, since they rely upon small sets of movable objects whose numerosity is perceivable in infancy, to support the acquisition of more abstract arithmetic computations.

Occasionally, however, some of the child's pre-existing cerebral representations may run counter to what needs to be learned. The necessity to unlearn features that were useful in our evolution, but are now counterproductive for the current cultural use of a given brain area, may explain the striking difficulties that some school topics pose to all children. In arithmetic, negative numbers and fractions are good examples of difficult concepts that may go significantly beyond the existing representational capacities of the preverbal primate brain, because they violate basic principles of integer arithmetic (for instance, that adding and multiplying always result in a larger number). Similarly in reading, letters that are mirror images of each other may pose a special challenge for our visual system. Inferotemporal neurons appear to generalize spontaneously across left-right symmetry, preferring the same

object whether it is facing left or right (Rollenhagen & Olson, 2000). Contrary to location and size invariance, this invariance across mirror symmetry, although useful in object recognition, may be deleterious for reading as it may lead to confusion of the letters p and q, or b and d. This may explain the peculiar errors that young children make, sometimes writing single letters or even entire words in mirror image without noticing it (Orton, 1925). If my hypothesis of a recyling of the ventral object recognition system for reading is correct, this form of mirror-image generalization needs to be unlearned during the acquisition of reading.

Prediction 3: Cultural learning may reduce the cortical space available for previous abilities. In many cases, cultural learning improves on an existing biological function. For instance, in the arithmetic domain, new symbolic and linguistic representations of numerals become connected to the analog quantity representation. These new connections make quantity information quickly available in a broad variety of multimodal contexts, and they may even improve the precision with which two numbers can be discriminated. In other cases, however, the invasion of an evolutionary older circuit by a new cultural tool may have a measurable cost. This may happen when the old and new functions are incompatible. In such cases, through competition for cortical space, the evolutionary older competence may be reduced or even lost. Learning to read, for instance, may partially displace and reduce object-related activations in the left inferotemporal sulcus. This should have a small cost on the speed or accuracy of visual recognition.

Such a competition effect may not be of much practical import, since it is likely to be detectable only under laboratory conditions. However, it would provide a clear test of the recycling hypothesis. While this prediction does not seem to have been evaluated in the reading domain, it may not be as implausible as it may seem. Indeed, acquisition of visual expertise for cars, which is known to engage inferotemporal cortex within or close to the fusiform face area, was recently shown to interfere with face perception. In comparison to

control subjects, experts in car recognition who were asked to memorize cars and faces on alternate trials showed evidence of reduced holistic processing of faces, both in behavioral performance and in the amplitude of the right-hemispheric face-evoked event-related potential (Gauthier, Curran, Curby, & Collins, 2003). If replicated, this result may indicate that the acquisition of car expertise interferes with some components of face recognition processes.

Conclusion

The "neuronal recycling" hypothesis emphasizes that cultural acquisitions must take place within the limited surface and bounded plasticity of the human cortex. The examples of reading and arithmetic indicate that there is more reproducibility in the cortical implementation of those functions than might have been expected based on standard assumptions of large-scale brain plasticity and inter-individual variability. A similar degree of anatomical regularity, indicating the existence of significant evolutionary precursors, may exist for other currently understudied cultural domains of human competence such as geometry, algebra, music, or art.

A basic issue remains: Why is it that among primates, only humans invent complex cultural systems such as reading and arithmetic? Various species of primates can be taught to recognize Arabic digits and map them onto quantities (Boysen & Berntson, 1996; Matsuzawa, 1985; Washburn & Rumbaugh, 1991). Thus, the crucial difference may not lie in the capacity to reconvert brain circuits through learning, but in the very ability to *create* new uses for evolutionary older circuits. According to a hypothesis exposed in detail elsewhere (Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001; Dehaene, Sergent, & Changeux, 2003), the radical expansion of prefrontal cortex and of cortico-cortical connections in our species (see e.g. Zilles, this volume) may have generated a new ability to mobilize existing processors in a top-down manner within a conscious neuronal workspace. This new circuitry would enable us to tentatively try out new mental syntheses and select them according to their

usefulness. Such mental flexibility might have been one of the key factors that lead our ancestors to first try connecting visual recognition processes with phonological and quantity representations, thus making the first crucial steps on the road to reading and arithmetic.

Acknowledgements

Figure legends

Figure 1. Core regions for number processing in humans. The image on top shows the intersection of activations observed in several tasks including number comparison, simple arithmetic, approximate calculation, and subliminal quantity processing (adapted from a meta-analysis in Dehaene, Piazza et al., 2003). Activations are systematically observed in the bilateral horizontal segment of the intraparietal sulcus (HIPS) as well as in precentral cortex. Caret software (Van Essen et al., 2001) was used to map the observed activations onto an unfolded map of the human cortex (only the right hemisphere is shown). For comparison, similar views of the macaque brain are shown, with white borders indicating the areas where neurons tuned to numerosity have been found (see Nieder & Miller, this volume). The human HIPS region, in the depth of the intraparietal sulcus, is a plausible homolog of the macaque area VIP. The human precentral activation is more distant from the monkey areas 45/46, suggesting a greater amount of distortion in prefrontal cortex during evolution, as also indicated by other comparative studies (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Nakahara, Hayashi, Konishi, & Miyashita, 2002).

Figure 2. Evidence for numerosity tuning in the human intraparietal cortex. Dehaene and Changeux's (1993) model of number processing postulated "numerosity-detector" neurons each tuned to an approximate numerosity (top), an hypothesis that was recently confirmed by single-neuron recordings in the monkey (see Nieder & Miller, this volume). A habituation design was used to probe the existence of a similar code in humans (middle). By repeatedly presenting a fixed numerosity (here 16) and then probing the fMRI response to various deviant numerosities, a tuning curve for numerosity change, here expressed as a Gaussian function of the log ratio of deviant to habituation number, could be observed in the HIPS region (bottom) (Piazza et al., submitted). This suggests a similar principle of number tuning in monkeys and humans.

Figure 3. Localization and properties of the human visual word form area. The VWFA is defined as a left occipitotemporal region activated in normal subjects in response to visual words more than to control stimuli (here, bright checkerboards); it is also the common lesion site for patients with pure alexia, a severe impairment in visual word identification (panel A, adapted from Cohen et al., in press). Invariance for case in this region can be demonstrated by using a subliminal priming paradigm, which shows case-independent repetition suppression of the BOLD response only in the left occipitotemporal sulcus (panel B, adapted from Dehaene et al., 2001). A plot of the latter activation on fiducial (left) and flattened (right) maps of a human left hemisphere (Caret software, Van Essen et al., 2001) indicates that this area lies just in front of area V8, within infero-temporal cortex involved in higher-level visual recognition.
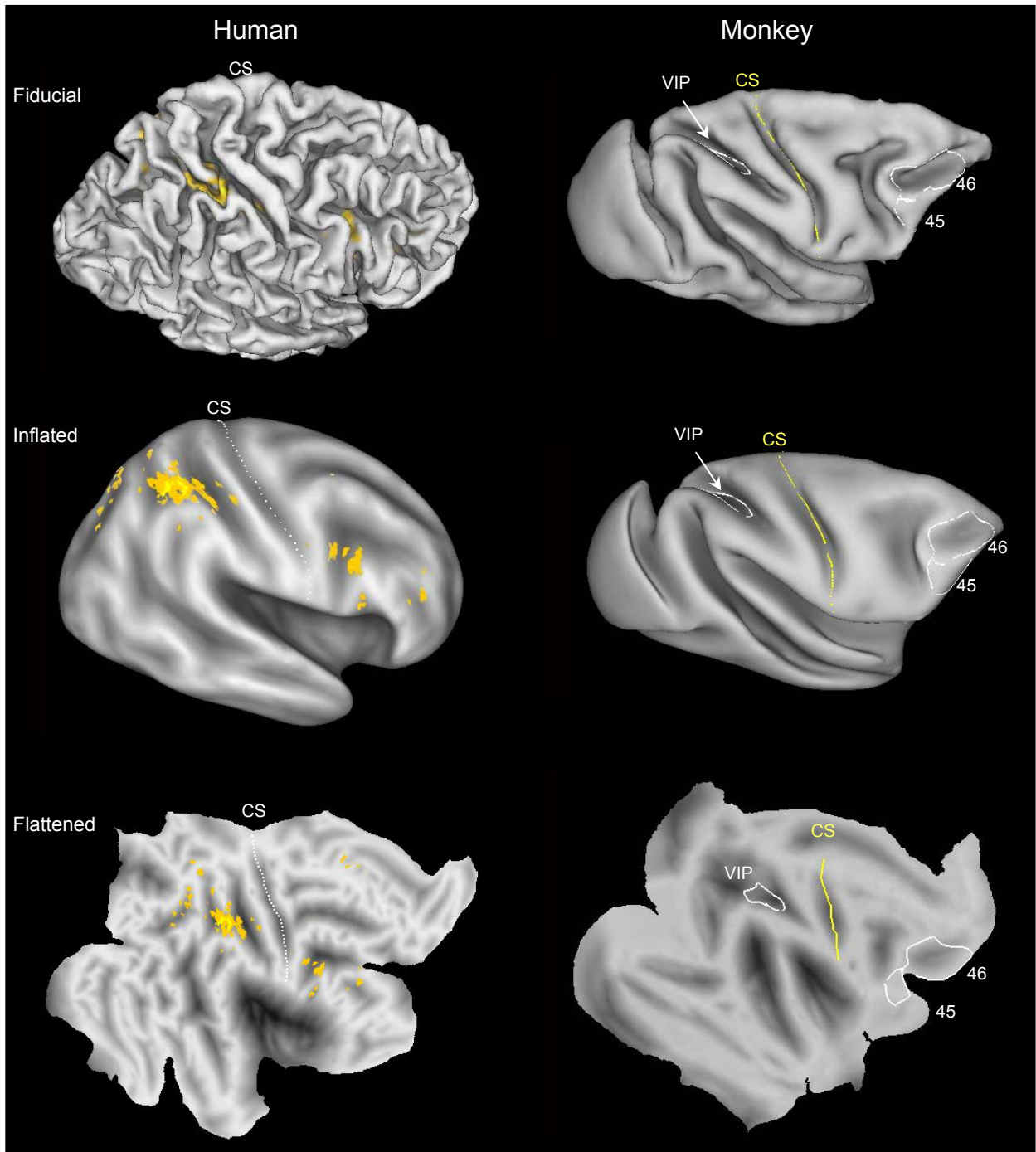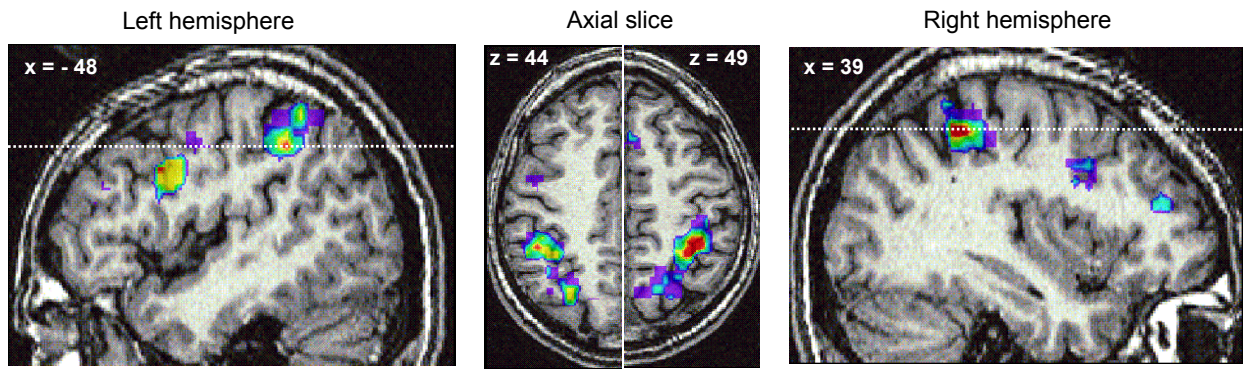
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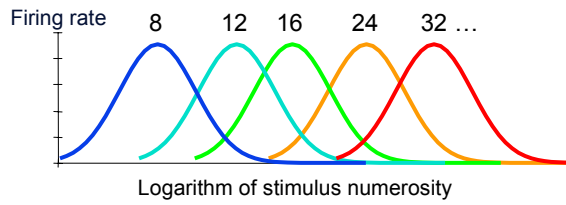
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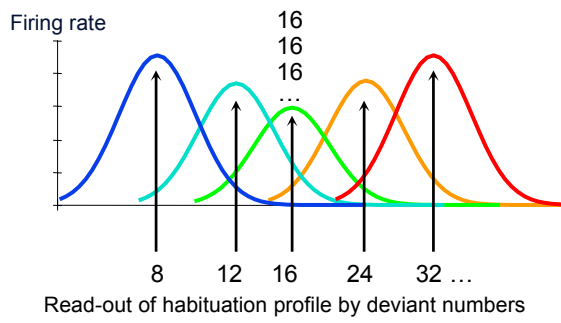
Left hemisphere   Axial slice   Right hemisphere

x = - 48   z = 44   z = 49   x = 39

Human   Monkey

CS   VIP   CS
Fiducial   46
                                                    45

CS   VIP   CS
Inflated   46
                                                    45

CS   CS
Flattened   VIP   46
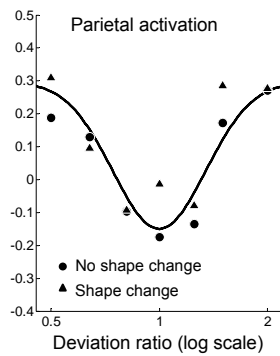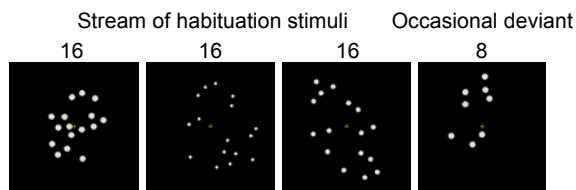   45

Dehaene, figure 1
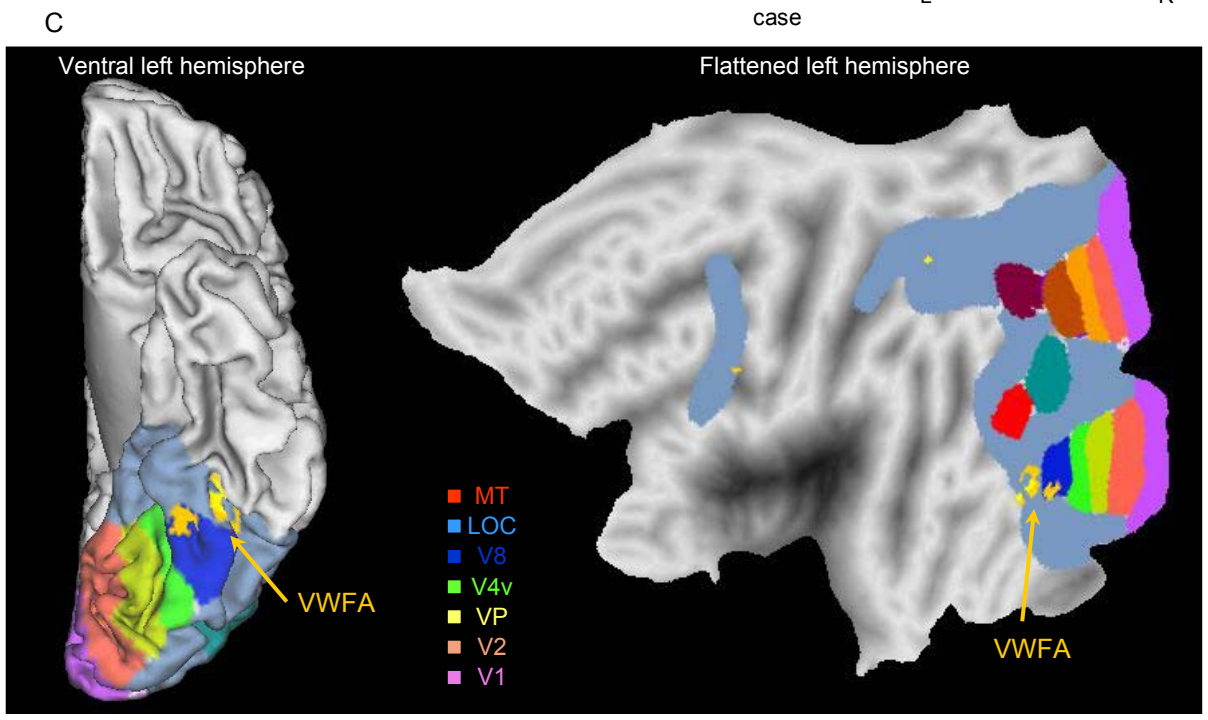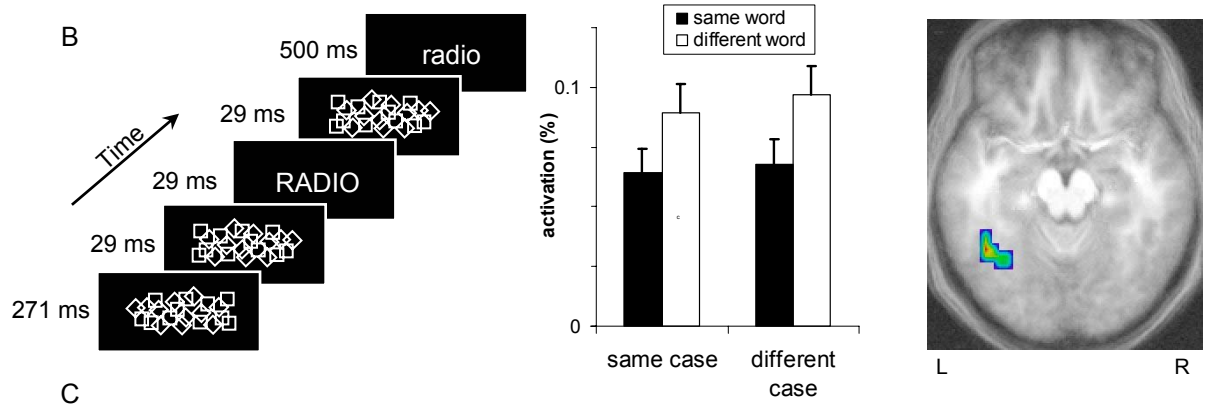
Numerosity detectors (Dehaene & Changeux, 1993)

Firing rate   8   12   16   24   32 …

Logarithm of stimulus numerosity

Habituation experiment

Firing rate

16
16
16
…

8   12   16   24   32 …

Read-out of habituation profile by deviant numbers

Stream of habituation stimuli   Occasional deviant

16   16   16   8

Parietal activation

● No shape change
▲ Shape change

Deviation ratio (log scale)

A

Activation in normal subjects

X = -38   Z = -14   Y = -63

Lesion overlap in pure alexia

B

Time

500 ms   radio
29 ms
29 ms   RADIO
29 ms
271 ms

- same word
- different word

activation (%)

0.1

0

same case   different case

L   R

C

Ventral left hemisphere   Flattened left hemisphere

- MT
- LOC
- V8
- V4v
- VP
- V2
- V1

VWFA   VWFA

Dehaene, figure 3