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Review

Cultural Recycling of Cortical Maps

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Part of human cortex is specialized for cultural domains such as reading and arithmetic, whose invention is too recent to have influenced the evolution of our species. Representations of letter strings and of numbers occupy reproducible locations within large-scale macromaps, respectively in the left occipito-temporal and bilateral intraparietal cortex. Furthermore, recent fMRI studies reveal a systematic architecture within these areas. To explain this paradoxical cerebral invariance of cultural maps, we propose a neuronal recycling hypothesis, according to which cultural inventions invade evolutionarily older brain circuits and inherit many of their structural constraints.

Introduction

The aim of the present paper is to briefly examine how fundamental elements of human culture, such as reading and arithmetic, are mapped at the cortical level. Over the past 20 years, brain imaging methods have yielded a large amount of data on how these cultural competences are represented in the adult and child brain. Here, we do not attempt to provide an exhaustive review, but rather ask how the relations between cultural and cortical representations should be theorized.

Although primitive cultural traits have been observed in nonhuman primate societies (Whiten et al., 1999), only humans experience a massive expansion of their evolutionary niche through cultural invention and transmission. By definition, cultural objects such as tools or writing systems are recent, optional, and acquired by learning. No selective pressure could have shaped the human brain to facilitate reading or high-level mathematics.

From this valid premise, several authors have jumped to the conclusion that the cultural competence of the human species must have arisen from the novel emergence of a vastly flexible domain-general learning capacity. This hypothesis, indeed, lies at the heart of the ‘‘standard social science model’’ shared by many anthropologists, sociologists, and some psychologists (see Barkow et al., 1992; and chapter 2 in Pinker, 2002), but also some neuroscientists who view the cortical surface as ‘‘largely equipotential and free of domain-specific structure’’ (Quartz and Sejnowski, 1997). Cortical expansion would have provided our species with more room for ‘‘instruction’’ by its cultural environment. *Homo sapiens* would therefore no longer owe its main dispositions to its biological architecture. Thanks to its plasticity, the human brain, more than that of any other animal species, would be capable of absorbing essentially any form of culture. It would therefore be meaningless, and a form of ‘‘category error,’’ to investigate the cortical constraints on cultural traits.

At variance with this viewpoint, we argue that the major domains of human cultural variability—including writing and arithmetic—are tightly constrained by our prior evolution and brain organization. In all cultures, these domains of knowledge map onto remarkably invariant brain structures that may aptly be called ‘‘cultural maps,’’ with only small cross-cultural variations. We propose that the paradoxical biological invariability of cultural maps can be resolved by examining how they arise by minimal transformation from cortical precursor maps present in other nonhuman primates.

The Neuronal Recycling Hypothesis

The model we have in mind is reminiscent of the concept of ‘‘exaptation’’ in evolutionary theory (Gould and Vrba, 1982)—the reuse, in the course of evolution, of an ancient biological mechanism in a completely different role. In cultural learning, however, this reuse obviously does not involve any genetic reshuffling, but occurs during the life span as a result of brain plasticity. The novel term ‘‘neuronal recycling’’ (Dehaene, 2005) was therefore introduced to refer to the putative mechanism by which a novel cultural object encroaches onto a pre-existing brain system.

The neuronal recycling hypothesis consists of the following postulates:

1. Human brain organization is subject to strong anatomical and connectional constraints inherited from evolution. Organized neural maps are present early on in infancy and bias subsequent learning.
2. Cultural acquisitions (e.g., reading) must find their ‘‘neuronal niche,’’ a set of circuits that are sufficiently close to the required function and sufficiently plastic as to reorient a significant fraction of their neural resources to this novel use.
3. As cortical territories dedicated to evolutionarily older functions are invaded by novel cultural

objects, their prior organization is never entirely erased. Thus, prior neural constraints exert a powerful influence on cultural acquisition and adult organization.

Those hypotheses lead to several predictions concerning cultural acquisition and its cerebral bases.

1. Variability in the cerebral representation of a cultural invention should be limited. Each cultural competence should be associated with one or several specific cortical maps, reproducibly located across individuals and across cultures. In turn, these cultural maps should be systematically related to precursor maps, present early on in human development and perhaps even in nonhuman primates, coding for an evolutionarily similar function.
2. Cultural variability should also be limited. Strong cross-cultural invariants should be identified, for instance across the world's writing systems (Changizi and Shimojo, 2005; Changizi et al., 2006), and ultimately traced back to neural constraints.
3. The speed and ease of cultural acquisition in children should be predictable based on the complexity of the cortical remapping required. This complexity should reflect two components: (1) the distance from the evolutionary precursor to the new function and (2) the intrinsic computational complexity of the cultural system (e.g., the degree of transparency of grapheme-phoneme relations [Ziegler and Goswami, 2005]). Prior cortical constraints should ultimately explain both the ease with which children acquire certain cultural tools and the specific difficulties that they occasionally meet. For instance, the systematic difficulty that children exhibit in discriminating mirror-image letters such as p and q may ultimately be traced back to the native propensity of our visual object recognition system for mirror-image generalization, due to its evolution in a world where the left-right distinction is largely irrelevant (Dehaene et al., 2005; Rollenhagen and Olson, 2000).
4. Although acculturation often leads to massive cognitive gains—for instance, literacy improves verbal memory and phonemic awareness (Morais and Kolinsky, 2005)—it might be possible to identify small losses in perceptual and cognitive abilities due to competition of the new cultural ability with the evolutionarily older function in relevant cortical regions. For instance, decreased symmetry perception may be one of the consequences of automatizing letter and word recognition in a single orientation (Danziger and Pederson, 1998; Lachmann and van Leeuwen, 2007).

Evidence in support of these predictions in the domain of reading acquisition is discussed in detail in a recent book (Dehaene, 2007a). In the present article, for lack of space, we concentrate mostly on prediction 1, namely the existence of relatively invariable cultural maps identifiable with neuroimaging methods.

Cultural Maps and Neuronal Recycling

It is useful to begin by clarifying our concept of cortical map as it applies to cultural objects. The concept of a ''map'' supposes that there is a lawful relation between the surface of cortex and a relevant aspect of the representational structure. In the simplest case, when the represented parameter belongs to a continuous metric space with one or two dimensions, an isomorphic continuous map may be found on the surface of cortex (e.g., retinotopy, tonotopy). More commonly, the represented domain has a complicated topological structure that cannot be isomorphically projected onto such a simple two-dimensional cortical map—yet there still exists a systematic ''mapping'' whereby each cortical column represents a specific dimension or parameter of the target domain, and nearby cortical locations frequently code for distinct but similar parameters. For instance, the space of recognizable visual shapes, although large, patchy, and multidimensional, maps onto the cortical surface of monkey inferotemporal cortex in a partially regular topological manner (Tanaka, 2003). Similarly, knowledge of cultural objects such as writing systems might be encoded in locally regular one-to-one mappings, for example, between individual letters and the surface of cortex (Dehaene et al., 2005).

The spatial scale at which these cortical mappings occur may vary and obviously plays a determinant role in our ability to detect them using the coarse tools of noninvasive human neuroimaging. One may distinguish, at the very least, an organization into *macro*maps, *meso*maps, and *micro*maps.

- Macromaps describe how brain areas are organized geometrically relative to each other, hence at the scale of one or several centimeters. At this scale, most heavily studied with PET and fMRI, several reproducible spatial patterns have been identified, for instance relating the activation evoked by written words to neighboring areas responsive to faces, objects, and houses (Gaillard et al., 2006; Hasson et al., 2002; Puce et al., 1996).
- ''Mesomaps'' characterize the global spatial structure *within* a given brain area (hence at the scale of millimeters or centimeters at most). Retinotopic and tonotopic areas provide good examples of mesomaps accessible with high-field fMRI (Formisano et al., 2003): in both cases, a parameter (location, pitch) is encoded by its location within a continuous structure covering the entire extent of a brain area.
- ''Micromaps'' refer to the finer-grained structure by which local cortical patches encode information. In V1, for instance, nested within the overall retinotopic mesomap, parameters such as line orientation or eye of origin are coded at the scale of individual cortical columns. We propose to call ''micromaps'' these structures that recur multiple times within

a cortical area, at a characteristic scale of a few hundred microns. The micromap concept is clearly the most speculative aspect of our proposal, for several reasons. In higher cortical areas, it remains unclear whether microstructures such as columns exist or whether neurons are randomly intermingled (but see Goldman-Rakic and Schwartz, 1982). Even in well-characterized cases such as ocular dominance columns, their functional role, if any, remains debated (Horton and Adams, 2005). Finally, even if human cortex contains columnar structures, it is unclear whether human neuroimaging will ever gain direct access to this representational level, beyond the simplest case of ocular dominance columns (Yacoub et al., 2007). At present, all fine-grained inferences about cortical coding in humans are based only on indirect evidence arising from fMRI priming, adaptation, or multivariate decoding techniques, neither of which addresses the columnar organization of cortex. Electrophysiological recordings, whether in monkeys or in humans (e.g., Quiroga et al., 2005), are likely to play an indispensable role in micromap characterization.

A key issue, finally, concerns the origins of maps in the human brain. The reproducibility of the cultural maps for reading and arithmetic imply that they ultimately originate from universal cortical biases that may themselves be imputed to two major sources of organization. First, patterns of gene expression may specify an early organization of the cortex into basic "morphogenetic maps"—large-scale structures (macromaps), perhaps created by diffusing molecules called morphogenes (Turing, 1952), that bias cortical regions to distinct functions. For instance, the large-scale division of cortex into visual, auditory, and tactile sectors likely originates from this level (Krubitzer and Kahn, 2003). Second, postnatal activity may refine these initial genetic biases and lead to detailed "epigenetic maps" that reflect the constraints and correlation structure of sensory inputs (Gilbert et al., 2001).

With these basic conceptual tools in mind, we now turn to a review of the evidence for cultural maps in two major domains of human culture: reading and arithmetic. In both cases, we start by reviewing brain imaging evidence for a systematic, culturally invariant mapping in human adults, first at the macromap level, then at the meso- and micromap levels. We then consider the possible evolutionary precursors of this organization, that is, the corresponding morphogenetic and epigenetic maps that predate cultural learning. Finally, we consider evidence for a process of neuronal recycling in the course of cultural acquisition in children.

Reading

Writing was invented around 5400 years ago by the Babylonians. Until very recently, only a very small fraction of humanity was able to read. Thus, it is logically impossible that human brain regions evolved specifically for the purpose of reading. It therefore comes as a surprise that several left-hemispheric regions are reproducibly activated during word reading (Bolger et al., 2005; Jobard et al., 2003; Petersen et al., 1988). Some of them are shared with spoken language processing, which may have enjoyed a species-specific evolution. However, one of them, which is the focus of this review, appears uniquely concerned with written as opposed to spoken word recognition (Dehaene et al., 2002). This highly reproducible activation site (Jobard et al., 2003), located in the left occipito-temporal sulcus, is easily identified by contrasting activations induced by strings of letters relative to rest or to low-level stimuli (Cohen et al., 2000, 2002), but also relative to other categories of visual objects such as faces or houses (Baker et al., 2007; Ben-Shachar et al., 2007; Hasson et al., 2002; Puce et al., 1996). This region has therefore been termed the visual word form area (VWFA), a label that should not be taken to imply that this cortical sector is entirely dedicated to reading, but solely that it comprises reproducible and specific neural mechanisms for recognizing written characters (Cohen and Dehaene, 2004; Cohen et al., 2000).

Cross-Individual and Cross-Cultural Consistency

The location of the VWFA is remarkably reproducible across subjects. It is always found at or around the lateral occipito-temporal sulcus, at approximate coordinates −44, −58, −15, with a standard deviation of about 5 mm (Bolger et al., 2005; Cohen et al., 2002; Jobard et al., 2003). This interindividual reproducibility is also accompanied by a remarkable cross-cultural consistency. Word-induced activation is found at or around the VWFA site in all good readers, regardless of the writing system they master. In an extensive overview, Bolger et al. (2005) found an average peak activation common to Japanese syllabic kana and logographic kanji stimuli (−43, −54, −12) within millimeters of the peak observed in Chinese readers (−49, −53, −10) and in readers of the Roman alphabet (−45, −56, −16).

This cross-cultural reproducibility would be trivial if the VWFA performed a generic visual function, for instance if it responded to any high-contrast intersection of lines. However, evidence suggests that it is functionally specialized for orthographic processing in the subject's script (Cohen and Dehaene, 2004). For instance, for identical stimuli, activation is stronger when the script used (Hebrew versus Roman alphabet) is familiar to subjects than when it is unfamiliar (Baker et al., 2007). Also, within the subjects' familiar script, the VWFA is activated more strongly by words or readable pseudowords than by consonant strings, showing that it has incorporated orthographic regularities (Cohen et al., 2002; Vinckier et al., 2007). Binder et al. (2006) recently showed that activation increases monotonically with bigram frequency in the left occipito-temporal region (but not the right), at the usual main peak of the VWFA, indicating a fine tuning to frequent letter combinations. Finally, using repetition priming, we showed that the VWFA computes a representation of printed words that is invariant for the upper versus lower case distinction (e.g., radio versus RADIO), another arbitrary cultural feature of our writing system (Dehaene et al., 2001, 2004). Thus, the VWFA develops an elaborate functional specialization during reading acquisition—yet this acquisition seems to be remarkably constrained within cortical space. Only small systematic cultural distinctions in the cortical localization of reading-induced activation have been observed. Activation is more bilateral and tends to be slightly more mesial for ideographic Chinese/Kanji scripts than for alphabetic or Kana scripts (Bolger et al., 2005; Nakamura et al., 2005). Within alphabetic script, activation is also more extended and lateral for English, an orthography with complex grapheme-phoneme relations, compared to Italian, a highly transparent script (Paulesu et al., 2000), compatible with the idea that a greater cortical territory must be devoted to more complex orthographies.

Macromap

The VWFA occupies a reproducible localization with an overall macromap of sensitivity to object categories in occipito-temporal cortex. Puce et al. (1996) were the first to demonstrate, using fMRI, that in all subjects, the peak activation evoked by written words in the left occipito-temporal sulcus is always slightly lateral to that evoked by faces. Since then, a reproducible organization of activations to houses, faces, and objects has been repeatedly observed, within which words occupy a fixed location (Gaillard et al., 2006; Hasson et al., 2002, 2003; Ishai et al., 1999) (Figures 1A and 1B). Intracranial studies confirm that individual sites can be remarkably selective for orthographic strings and that their cortical distribution, although patchy and variable, presents reproducible statistical features across individuals (Allison et al., 1994).

The causal role of the VWFA region in reading cannot be established by neuroimaging but is supported by lesion studies. Intersection of the MR-defined lesions of several patients points to the VWFA site as a crucial region for reading deficits (Cohen et al., 2003; Philipose et al., 2007). Recently, we studied changes in the fMRI macromap for words, faces, houses, and tools before and after a small surgical occipito-temporal lesion, aimed to prevent epilepsy, caused pure alexia in a previously normal reader. Although the lesion was posterior to the VWFA, it led to the selective disappearance of the word-induced VWFA activation, presumably by specific disconnection, with a preservation of the rest of the occipito-temporal mosaic activated by faces, houses, and tools.

Meso- and Micromaps

Is there an internal mesomap structure *within* the visual word form area? Electrophysiological data in macaques show that the ventral visual system harbors a posterior-to-anterior hierarchy of converging neural detectors with progressively larger receptor fields, tuned to increasingly complex objects or fragments of objects (Booth and Rolls, 1998; Rolls, 2000). We hypothesized that visual word encoding in humans may obey this general principle. Specifically, our model proposes that words are encoded in the VWFA through a hierarchy of neurons functioning as ‘‘local combination detectors,’’ each tuned to increasingly larger and more complex fragments of words such as line intersections, letter shapes, case-invariant letter identities, bigrams (ordered letter pairs), and morphemes (Dehaene et al., 2005). At each of these levels, the model supposes that, as a result of exposure to print, neural detectors have become dedicated to the recognition of frequent fragments that are useful to encode existing words.

To probe this putative hierarchy, we recently scanned adult French readers with fMRI while they were exposed to strings of letters with an increasing structural similarity to real words, including strings of infrequent letters, strings of frequent letters but rare bigrams, strings with frequent bigrams but rare quadrigrams, strings with frequent quadrigrams, and real words (Vinckier et al., 2007). We found that activations pooled over the whole VWF system increased for stimuli forming closer statistical approximations to real words, a result congruent with Binder et al. (2006). Most relevant to the issue of mesomaps, we observed a spatial gradient structure within the VWFA: the more anterior a voxel is within the VWFA, the more selective it is to letters strings comprising complex and frequent components (Figure 1C). The most posterior fusiform region ($y = -96$) was activated equally by all types of stimuli. The next more anterior region ($y = -80$) showed the first indication of a hierarchical preference for stimuli according to their proximity to real words. This functional hierarchy then increased steadily to the most anterior region ($y = -40$).

Moving now to the micromap level, fMRI currently cannot resolve the postulated fine-grained mosaic of neurons sensitive to letters, bigrams, and morphemes. However, the fMRI priming or adaptation method allows probing the neuronal coding of letter strings indirectly through the measure of repetition suppression (although without being able to reveal its putative columnar structure). Using a subliminal priming design, Dehaene et al. (2004) have begun to show that the type of prime-target similarity that causes fMRI repetition suppression varies according to the anterior-posterior location in left ventral cortex. In the most posterior region, priming depended on the repetition of the same letters at the same location, consistent with a dominance of location-specific but case-independent letter detectors. At an intermediate location, priming resisted to a shift of one letter location, suggesting increased spatial invariance. Finally, at a more anterior location, priming became dependent on the similarity of the entire prime and target strings (and thus reduced for anagram pairs such as range/anger), suggesting greater reliance on larger size, order-dependent units such as bigrams or morphemes.

Altogether, these priming results suggest the existence of a specific neural code for letter strings, including neurons specific both to a letter and to a location. One might further speculate that, at a submillimetric scale, neurons tuned to different letters or different bigrams entertain

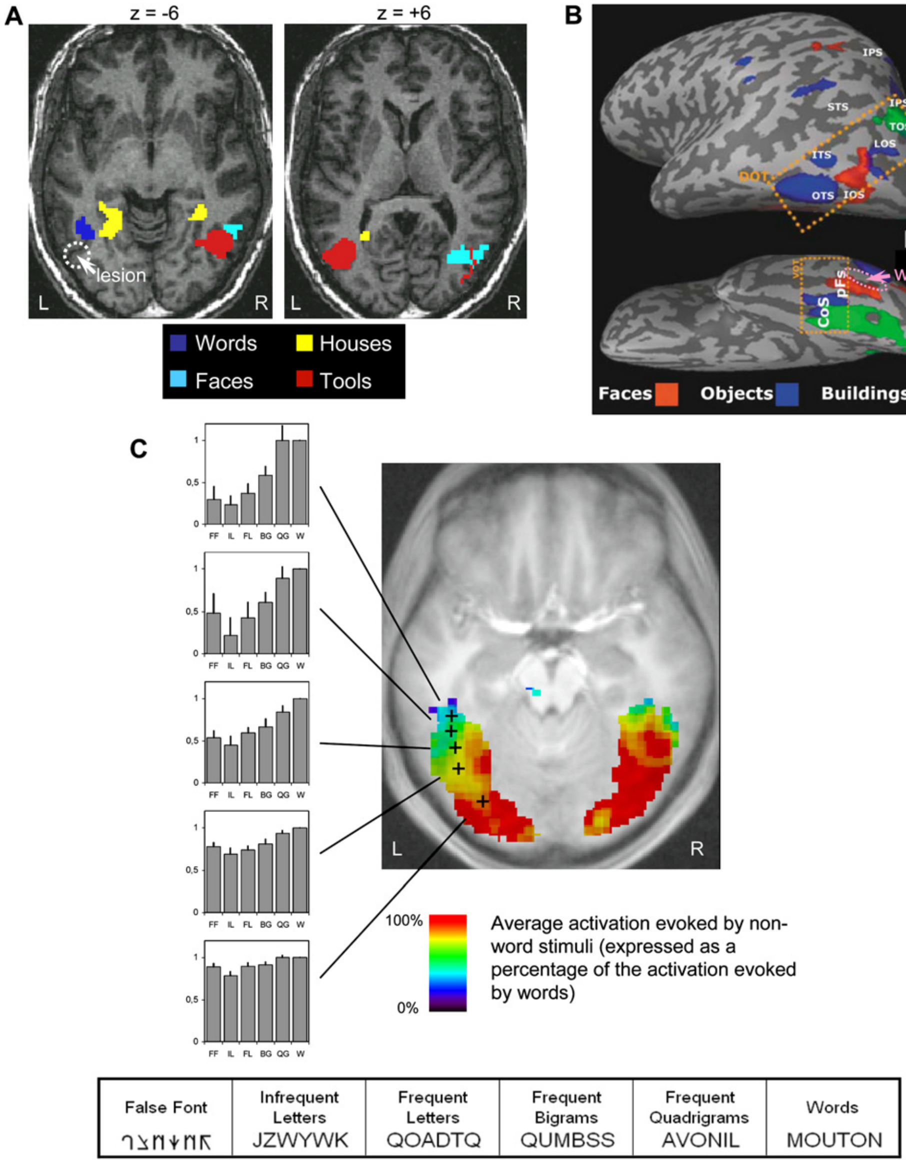

Figure 1. Macromap and Mesomap Associated with Reading Expertise in the Left Occipito-Temporal Cortex (Visual Word Form Area [VWFA])

(A and B) Insertion of activation evoked by written words within a larger-scale map of object preference in ventral and dorsal occipito-temporal cortex. Panel (A) shows categorical preference in a single subject with epilepsy (from Gaillard et al., 2006). Later surgical removal of the marked region resulted in pure alexia and selective disappearance of the word-induced activation, establishing the causal role of the VWFA in reading. Panel (B) shows how this region occupies a reproducible localization within the group-average macromap of preference for faces, objects, and buildings (from Hasson et al., 2003). Panel (C) shows a recently discovered mesomap organization within the anterior-posterior extent of the VWFA: increasingly closer orthographic approximations of words lead to increasingly anterior activation in left but not right occipito-temporal cortex (from Vinckier et al., 2007).

nonrandom spatial relationships, by analogy with the observation that in monkeys contiguous inferotemporal cortical columns tend to be tuned to similar elementary shapes, several of which resemble letters (Tanaka, 2003). This putative micromap remains out of reach, although it may ultimately become accessible using intracerebral single-unit recordings (Quiroga et al., 2005).

An interesting prediction of the neuronal recycling hypothesis, is that meso- and micromaps for visual word recognition share universal principles of organization across cultures. Even in nonalphabetic systems such as Chinese, it should therefore be possible to find an anterior-to-posterior gradient of sensitivity to character fragments of increasing size and relevance to semantic and phonological access. Although this prediction has not been tested yet, behavioral priming studies indicate that Chinese characters are not recognized as holistic wholes, but are decomposed into subelements such as radicals, some of which are associated with location-specific detectors (Ding et al., 2004) Furthermore, effects of character frequency and of consistency of orthography-to-phonology mapping have been observed, leading to the conclusion that ''the neuronal mechanisms for orthography-to-phonology transformation [are] domain universal across different writing systems'' (Lee et al., 2004).

Morphogenetic and Epigenetic Precursors

What evolutionary precursors could explain the remarkable consistency in cortical localization and organization of orthographic processing across cultures? At least three principles of cortical organization, by their joint constraints, could bias the VWFA to a reproducible brain localization. First, as noted above, its posterior-to-anterior extension is consistent with a principle of increasingly invariant hierarchical coding common to all primates (Booth and Rolls, 1998; Rolls, 2000) and observed in humans using fMRI during visual recognition of increasingly scrambled images (Grill-Spector et al., 1998; Lerner et al., 2001). Second, as concerns its lateral position, Hasson, Malach, and collaborators have noted that the VWFA, like the fusiform face area (FFA), occupies a precise position within a large-scale gradient of preference for foveal versus parafoveal presentation of visual stimuli (Hasson et al., 2003; Malach et al., 2002). Words and faces land at a lateral occipito-temporal localization biased for foveal stimuli, consistent with the need for high spatial accuracy in deciphering the fine details of these stimuli. Both lateral and antero-posterior gradients are major structures, cutting across several brain areas, that could be laid down pre- or perinatally by diffusing morphogenes according to Turing's (Turing, 1952) model.

Third, one must still explain why the VWFA is always consistently lateralized to the left hemisphere. Two mutually compatible suggestions can be made. First, the left visual occipito-temporal cortex may be selected because it provides shorter, more direct connections to language areas than the corresponding right-hemispheric regions. Indeed, the projection field of the VWFA site may be ideally suited for projection to other temporal language sites, as it lies in the depth of the lateral occipital-temporal sulcus and thus spatially very close or even abutting to middle temporal language regions (Cohen et al., 2004). Consistent with this possibility, the VWFA colateralizes with more anterior language processing sites involved in verb generation (Cai et al., 2007). However, one cannot exclude that another bias for VWFA lateralization arises from purely visual interhemispheric differences: reading may require an analytic, fine-grained mode of recognition for which the left hemisphere seems intrinsically superior (Kitterle and Selig, 1991).

According to the neuronal recycling hypothesis, cortical biases constraint visual word recognition to a specific anatomical site, but they may even have exerted a powerful constraint, during the evolution of writing systems, on the very form that these systems take, thus reducing the span of cross-cultural variations. Consistent with this view, Changizi and collaborators have recently demonstrated two remarkable cross-cultural universals in the visual properties of writing systems (Changizi and Shimojo, 2005; Changizi et al., 2006). First, in all alphabets, letters are consistently composed of an average of about three strokes per character (Changizi and Shimojo, 2005). This number may be tentatively related to the visual system's hierarchical organization, where increases in the complexity of the neurons' preferred features are accompanied by a 2- to 3-fold increase in receptive field size (Rolls, 2000). Inferotemporal neurons are thought to gain their sensitivity to complex shapes by pooling over neurons coding for simpler shapes at the immediately earlier level (Brincat and Connor, 2004; Serre et al., 2007). Assuming that this pooling occurs within a radius of about three receptive fields, elementary letter shape would only be recognized as combinations of about three simpler strokes, thus accounting for Changizi's ''magic number'' (Changizi and Shimojo, 2005). This account might be extended to other levels of the word recognition system (Dehaene, 2007a; Dehaene et al., 2005). Upstream of the single-letter level, the elementary strokes used in the world's writing systems may themselves be composed of approximately three line segments. Downstream of it, it may be suggested that writing makes frequent use of combinations of two to four letters as morphemes (prefixes, suffixes, or word roots). Chinese characters also typically combine two to four functional subelements (Ding et al., 2004). These predictions, however, still await quantitative confirmation.

A second cross-cultural universal is that, in all writing systems, topological intersections of contours (e.g., T, Y, L, Δ) recur with a universal frequency distribution (Changizi et al., 2006). Remarkably, these intersections are not typically observed in random images, but occur with the same frequency in natural images (Changizi et al., 2006). Many of these intersections signal ''nonaccidental properties'' that denote important and invariant connection and occlusion relations (Biederman, 1987) and are already encoded in monkey infero-temporal cortex (Kayaert et al., 2005). Thus, the suggestion is that, while the occipito-temporal cortex could not evolve for reading, the shapes used by our writing systems were submitted to a cultural evolution for faster learnability by matching the elementary intersections already used in any primate visual system for object and scene recognition.

Evidence for Cultural Recycling

How is the adult macromap for words and other categories of visual stimuli established during development? Answering this question requires the development of better imaging methods in early childhood. At present, only a handful of studies are available, mostly at later ages (>9 years) corresponding to late automatization rather than early reading acquisition (review in Schlaggar and McCandliss, 2007). These studies suggest increasing VWFA responses, tightly correlated with reading performance (Shaywitz et al., 2002), with a concomitant decrease in right-hemisphere visual responsiveness (Turkeltaub et al., 2003). A recent

ERP study (Maurer et al., 2006) captured the early stages of this progressive convergence process by comparing kindergartners (nonreaders), second graders, and adults. A greater N170 ERP component to words than to unknown symbol strings appeared during reading acquisition. In second graders, this response was larger and more bilateral than the focused left-lateralized response seen in adults. Altogether, this evidence is compatible with a slow search process whereby reading expertise is initially unfocused in the ventral visual system and progressively finds its ''optimal'' location at the left VWFA site, when cortical tissue is slowly recycled to ultimately become specialized, at least in part, for a specific writing system.

Arithmetic

The arithmetic tools that we use during routine calculation with Arabic numerals, such as 3 × 8 or 13 − 7, are even more recent cultural inventions than our reading systems. Positional numeration was first created in India around the 6th century A.D. and was imported into the Western world, together with calculation algorithms, during the middle ages via the treatises of Arab scientists. In spite of this recent history, mental arithmetic is a second cultural domain in which neuroimaging techniques have revealed a remarkable degree of cross-cultural consistency at the cerebral level.

Cross-Individual and Cross-Cultural Consistency

The first imaging studies of calculation, using SPECT, PET, and fMRI, quickly pointed to a reproducible bilateral parietal activation (Rueckert et al., 1996; Dehaene et al., 1996; Roland and Friberg, 1985). The advent of single-subject fMRI demonstrated that, although interindividual variability is somewhat larger than in studies of reading, the banks of the intraparietal sulcus are always consistently activated whenever adults compute simple comparison, addition, subtraction, or multiplication with Arabic numerals (Chochon et al., 1999).

Initial studies probed the exact nature of the contribution of this region to number processing. Intraparietal activation was observed during a great variety of number-related tasks, including calculation but also larger-smaller comparison (Pinel et al., 2001) or even the mere detection of a digit among colors and letters (Eger et al., 2003). The intraparietal region seems to be associated with an abstract, amodal representation of numbers inasmuch as it can be activated by numbers presented as concrete sets of visual or auditory objects and events (Castelli et al., 2006; Piazza et al., 2004, 2006, 2007) as well as in various culturally learned symbolic notations such as Arabic numerals and spelled-out or spoken number words (Eger et al., 2003).

Similar results have been consistently observed in experiments with adults from various countries and cultures, including France, UK, USA, Austria, Singapore, China, and Japan. In a direct comparison of Chinese and English speakers, Tang et al. (2006) observed intraparietal activation at a similar location in the IPS during calculation and comparison tasks. They did however observe cultural variation in other surrounding areas, particularly in left premotor cortex (more active in Chinese subjects) and left perisylvian areas (more active in English subjects). fMRI studies have demonstrated that the intraparietal sulcus is most activated during tasks that call upon abstract quantity manipulations, such as addition approximation or subtraction, whereas another circuit involving the left angular gyrus and/or surrounding perisylvian cortices shows greater activation during operations of exact calculation that depend on explicit education (Pica et al., 2004) and often rely on language-specific rote memorizing (Dehaene et al., 1999; Lee, 2000; Venkatraman et al., 2006). During training, activation progressively shifts from the parietal region to the angular gyrus as subjects commit arithmetic facts to a verbal memory (Delazer et al., 2003; Ischebeck et al., 2006). Altogether, therefore, those results mesh well with the notion of a core system of number, associated with the bilateral intraparietal cortex and invariable across cultures, and a distinct perisylvian circuit associated with language- and education-specific strategies for storing and retrieving arithmetic facts (Dehaene and Cohen, 1995).

Macromap

The parietal activation putatively associated with core ''number sense'' occupies a fixed location within an overall macromap of sensory, motor, and attentional functions in the parietal lobe (Figure 2). Our group used fMRI to study the cerebral organization of six different functions previously associated with parietal systems: finger pointing, manual grasping, visual attention orienting, eye movement, written word processing, and calculation (Simon et al., 2002, 2004). All subjects showed a reproducible geometrical layout of activations associated with these functions in the parietal lobe (see Figure 2). Most notably, activation uniquely evoked by calculation was observed in the depth of the intraparietal sulcus and was surrounded by a systematic front-to-back arrangement of activation associated with grasping, pointing, attention, eye movement, and language-related activations. The systematicity of this surrounding macromap was confirmed by subsequent research using more selective experiments specifically designed to isolate grasping, saccade, and attention-related functions (for review, see Culham et al., 2006).

Meso- and Micromaps

The search for a mesomap, a systematic organization of number-related activation *within* the IPS, has not met with much success yet. For instance, intraparietal activations during judgments of number versus other continuous dimensions such as physical size, angle, or luminance do not cluster neatly into distinct regions specific for a given quantitative parameter, but show considerable overlap (Cohen Kadosh and Henik, 2006; Fias et al., 2003; Pinel et al., 2004). Likewise, attempts to discover a ''numerotopic'' organization whereby representations of small and large numbers would be clustered at distinct locations,

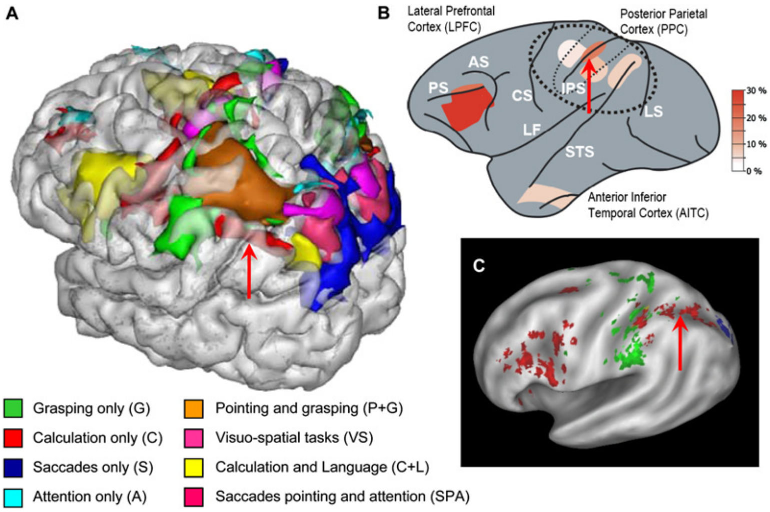

Figure 2. Insertion of Brain Activation Associated with Number Processing within a Parietal Macromap

(A) Human map of fMRI activations observed during six distinct tasks (after Simon et al., 2002, 2004). Activation during mental subtraction of Arabic numerals is inserted within a reproducible arrangement of regions associated with grasping, pointing, saccades, and attention. Part of this arrangement is reproduced in panel (C) on an unfolded view of the human brain (from Hubbard et al., 2005). The organization of grasping, arithmetic, and saccade activations resembles, in expanded and distorted form, the basic layout of areas AIP, VIP, and LIP in the macaque monkey. Panel (B) shows regions where neurons tuned to numerosity of sets of dots were recorded in the macaque monkey (from Nieder and Miller, 2004). The number neurons that were recorded in the fundus of the intraparietal sulcus, at or near area VIP, may constitute a precursor of the human ability for symbolic arithmetic.

thus forming a literal "number line" or map on the cortical surface, have been inconclusive so far (S.D. and A. Jobert, unpublished data). The current thinking, based on those results, is that neuronal populations coding for number are highly distributed in the intraparietal sulcus and are intertwined and overlapping with representations of other quantitative parameters (Pinel et al., 2004)—a conclusion supported by recent monkey physiology (Tudusciuc and Nieder, 2007, see below).

The method of fMRI adaptation, while unable to reveal a spatial cortical organization, has been used to indirectly demonstrate that the human intraparietal cortex must contain specialized neural populations coding for specific numbers (Naccache and Dehaene, 2001; Piazza et al., 2004, 2007). In those experiments, subjects were first adapted to the repeated presentation of a specific numerosity (e.g., many sets of 16 dots), then were probed with presentation of novel numerosities. A specific recovery signal was observed in the bilateral intraparietal sulcus whenever number change exceeded a minimal value. The profile of recovery was compatible with the existence of tuned neurons sensitive to an approximate number and with a fixed Gaussian variability on a logarithmic scale, in agreement with Weber's law (Piazza et al., 2004). Crucially, similar adaptation was also found during adaptation with symbolic numerals (Naccache and Dehaene, 2001) and from numerals to dots or vice-versa (Piazza et al., 2007). This observation suggests that our understanding of the cultural symbols of numbers is grounded in links with neurons coding for specific nonsymbolic numerosities in intraparietal cortex (Piazza et al., 2007; Verguts and Fias, 2004).

Putative Evolutionary Precursors

When the human parietal macromap for number and other sensori-motor functions was first published (Simon et al., 2002), we noted that the layout of eye, attention, and hand-related activation bore similarity with the anatomical organization of areas V6a, LIP, PRR, and AIP in macaques. Although details of this homology remain debated (Culham et al., 2006; Orban et al., 2006), the human macromap predicted that, if a precursor of human numerical abilities existed in monkeys, it might lie in the depth of the intraparietal sulcus. Indeed, shortly thereafter, awake-monkey electrophysiology uncovered number-coding neurons distributed within and near the intraparietal sulcus (Nieder and Miller, 2004; Sawamura et al., 2002). Although similar neurons were also found in the prefrontal cortex (Nieder et al., 2002), they responded with a longer latency and showed greater delay-related activity, suggesting that the parietal neurons constitute a primary numerosity code that prefrontal neurons held on-line during the delayed match-to-sample task.

Several parallels between monkeys and humans suggest that the monkey intraparietal neural code for numerosity may be the evolutionary precursor onto which the human invention of arithmetic encroached. First, numerosity-tuned neurons are mostly found in the depth of the intraparietal sulcus and often show visual flow-field responses, compatible with a location in area VIP (Tudusciuc and Nieder, 2007). Likewise, human fMRI studies have located a plausible homolog of area VIP (Bremmer et al., 2001; Sereno and Huang, 2006) at a location remarkably close and overlapping with that of number-related responses (see Hubbard et al., 2005). Second, monkey intraparietal neurons are each tuned to a particular numerosity and show Gaussian variability on a log scale (Nieder and Merten, 2007; Nieder and Miller, 2003, 2004), similar to inferences derived from behavioral and fMRI adaptation studies in humans (Piazza et al., 2004, 2007). Mathematical modeling indicates that, starting from the hypothesis of log-Gaussian neural coding and principles of optimal Bayesian decision making, the main characteristics of human behavior in simple arithmetic tasks can be reproduced (Dehaene, 2007b). Third, in some neurons at least, the code is abstract enough to respond to both sequential and simultaneous presentations of number (Nieder et al., 2006). Fourth, distinct but intermingled populations of neurons code for number and line length (Tudusciuc and Nieder, 2007), again as inferred from human fMRI (Pinel et al., 2004).

Recently, Roitman et al. (2007) uncovered another type of neural code for numerosity in area LIP. Here, firing rate varies monotonically with numerosity, either increasing or decreasing sharply with the logarithm of the number of objects in the neuron's receptive field. Neural network models suggest that such monotonic coding may be needed as an intermediate step in the extraction of an abstract numerosity code from an input retina where objects of different sizes are presented (Dehaene and Changeux, 1993; Verguts and Fias, 2004). Interestingly, the putative human homolog of area LIP is also active during some number processing tasks (Dehaene et al., 2003), fuelling the speculation that the VIP-LIP circuitry is partially recycled for mental arithmetic in humans (Hubbard et al., 2005). The VIP-LIP circuit plays a particular role in updating internal representations of space during eye movements (Duhamel et al., 1992; Medendorp et al., 2003), an operation of vector addition that is formally analogous to approximate arithmetic. Thus, the numerical sensitivity of areas VIP and LIP as well as the spatial transformations they perform may have constituted evolved properties that provided a precursor for their later recycling for symbolic arithmetic in our species.

Evidence for Cultural Recycling

Even very young children show a sensitivity to numerosity and to concrete addition and subtraction operations performed on sets (Berger et al., 2006; for review, see Feigenson et al., 2004). Number-related parietal activation, particularly in the right hemisphere, is already present in 4-year-old children as they attend to the numerosity of sets (Cantlon et al., 2006; Temple and Posner, 1998). Thus, the parietal mechanism of numerosity extraction identified in monkeys seems to be already functional prior to arithmetic education in humans.

An important test of the neuronal recycling hypothesis would be to show that this system is actively changed during arithmetic education. Unfortunately, few fMRI studies have examined changes in brain activity associated with the acquisition of symbolic arithmetic. Those studies point to left parietal cortex as a crucial site for arithmetic development, compatible with the hypothesis that this region serves as a hub where abstract quantity information meets with left-hemispheric codes for Arabic and verbal number symbols (Dehaene and Cohen, 1995). Ansari and Dhital (2006) observed a greater effect of the distance between numbers during a comparison task in this region in adults compared to 10-year-olds, suggesting an increasing involvement of this region with increasing age. Rivera et al. (2005) found that, during mental arithmetic in 8- to 19-year-olds, left parietal activity increased with age together with left inferior occipito-temporal cortex, compatible with a strengthening of the links between the visual form of Arabic numerals and the corresponding quantities. Interestingly, a massive decrease was observed in prefrontal activity, suggesting that the automatization of mental arithmetic is accompanied by a progressive transfer from anterior generic to posterior specialized circuits.

Very recently, Diester and Nieder (2007) presented the first electrophysiological study of symbol acquisition in monkeys. They trained two monkeys to match the shapes of Arabic numerals 1–4 with the corresponding numerosities of sets. Recordings identified numerosity-tuned neurons in both notations, but the vast majority of parietal neurons were specialized either for Arabic numerals or for numerosities, not both. Only in dorsolateral prefrontal cortex was a substantial population of neurons tuned similarly to symbolic and nonsymbolic number. This finding suggests that only prefrontal cortex is initially capable of encoding the arbitrary relation between symbols and their numerical meaning. In humans, considerable training may ultimately lead to a transfer to specialized posterior brain systems.

One last indication in support of the recycling model, confirming that the prior organization of parietal areas plays a significant role in the acquisition of formal arithmetic in children, comes from studies of variability in arithmetic performance. A recent behavioral study shows that, prior to any explicit instruction, preschoolers possess a spontaneous capacity for approximate symbolic arithmetic whose variability is predictive of subsequent success in the math curriculum (Gilmore et al., 2007). At one extreme of variability, some children suffer from dyscalculia, a disproportionate impairment in learning arithmetic which cannot be imputed to general intelligence, sensorimotor deficit, or deficient social or educational background. MR studies have revealed that some of these children suffer from parietal hypoactivation and anatomical disorganization (Barnea-Goraly et al., 2005; Eliez et al., 2001; Isaacs et al., 2001; Kucian et al., 2006; Levy et al., 1999; Molko et al., 2003). These alterations are often due to genetic pre- or perinatal pathologies, suggesting that they may represent plausible causes rather than consequences of dyscalculia. Thus, those results suggest that availability of a functional parietal quantity system is an essential prerequisite for arithmetic development.

General Discussion

The two examples that we have analyzed here, reading and arithmetic, possess both similarities and differences. In both cases, arbitrary cultural symbols are associated with a reproducible cerebral substrate that occupies a well-defined location on the cortical macromap in all individuals and all cultures tested so far. In both cases, a plausible evolutionary precursor has been identified in nonhuman primates, and the detailed organization of human cultural systems has begun to be related to the characteristics of neuronal tuning functions in monkeys. There is however an important difference between arithmetic and reading. On the one hand, knowledge of number may have been selected for during primate evolution, because of the importance of keeping track of quantities of food or number of congeners (Flombaum et al., 2005). Intraparietal cortex is already engaged in number representation in primates, and the cultural mapping of number symbols onto this representation significantly enhances, but may not radically modify its representational capacity. On the other hand, the evolutionary precursor of the visual word form area is initially unrelated to reading. It relates to object and scene recognition, a function significantly different from the mapping of written language onto sound and meaning.

In general, we expect the most interesting cases of cultural neuronal recycling to be of the latter kind: extension of human brain abilities in a radically novel direction, not anticipated by evolution, but made possible by a cultural invention that cleverly exploits our cortical circuitry. In this conclusion, we briefly examine several examples that may be worth pursuing, although none of them has been submitted yet to the same kind of thorough examination as arithmetic and reading.

Speech Comprehension

A particularly debated case is to what extent the uniquely human capacity for speech results from a specifically human evolution or from processes of cultural innovation without a change in the genome (for review, see chapters in Christiansen and Kirby, 2003). In terms of macromaps, listening to stimuli in the subject's first language activates a highly reproducible array of regions along the superior temporal sulcus and with a significant left lateralization (Binder et al., 2000; Dehaene et al., 1997; Humphries et al., 2006; Mazoyer et al., 1993; Pallier et al., 2003). A hierarchical temporal organization has recently been described within this system: the phase of the activation in response to a single sentence systematically increases as one moves from the primary auditory cortex, either posteriorly toward Wernicke's area, or anteriorly toward the temporal pole (Dehaene-Lambertz et al., 2006a). Remarkably, this mesomap organization is already present in 2- to 3-month-old infants (Dehaene-Lambertz et al., 2006b) (Figure 3). Given the size of the delays involved (several seconds), the observed organization is unlikely to solely reflect synaptic delays, but has been interpreted as reflecting the increasing temporal span over which different areas integrate the incoming speech signal. An early bias, possibly of morphogenetic origin, for different areas of the temporal lobe to integrate speech inputs over segments, syllables, words, or phrases seems to predate the subsequent specialization of these areas for phonological, lexical, or syntactic integration. Although this bias might be a uniquely human evolution, the hierarchical architecture of the human temporal lobe presents numerous homologies to that of the monkey brain (Kaas and Hackett, 2000; Pandya and Yeterian, 1990), and a functional hemispheric asymmetry may already be present in nonhuman primates (Ghazanfar and Hauser, 1999; Poremba et al., 2004). Thus, the possibility exists that human speech and communication recycles a pre-existing primate system for hierarchical auditory representation, initially nonspecialized for speech processing. Fritz et al. (2005) further speculate that, within this largely conserved cortical architecture, auditory long-term memory may be the essential added ingredient that differentiates humans from other primates.

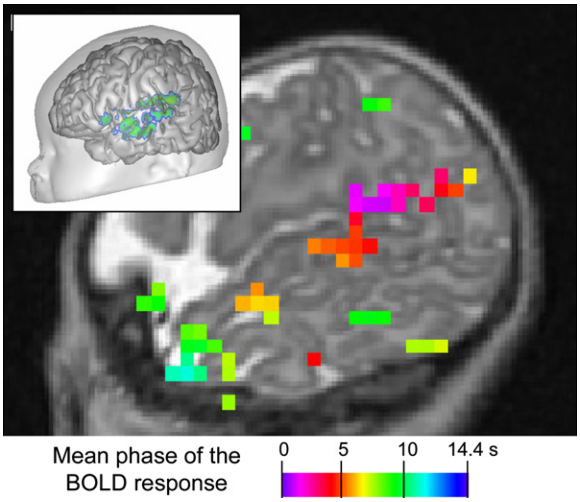

Figure 3. A Possible Morphogenetic Precursor of the Adult Macromap for Language in Left Perisylvian Cortex
The figure shows fMRI measurements of the phase of evoked responses to a single sentence in the left hemisphere of 3-month-old infants (after Dehaene-Lambertz et al., 2006b). A systematic gradient of response delays is found, with fast on-line responses near Heschl gyrus (purple) and increasingly slower responses as one moves either back into the *planum temporale* and Wernicke's area or forward along the STS toward the temporal pole and Broca's area. A similar arrangement is found in adults (Dehaene-Lambertz et al., 2006a), where it cannot be attributed purely to synaptic or hemodynamic delays, but may reflect integration and closure of speech segments of different lengths (phoneme, syllable, word, whole phrase). The presence of this gradient in very young infants, prior to any babbling, and its similarity to the hierarchical organization of anatomical projections in other primates (Kaas and Hackett, 2000; Pandya and Yeterian, 1990), suggests that it may constitute an innate bias that constrains language acquisition to a nested hierarchical structure.

Tool Use

Another essential dimension of human cultures, which has been particularly emphasized in a paleo-anthropological context, is the extension of human manual dexterity through the invention of tools. Knowledge and use of tools is associated with a universal cerebral substrate in left anterior parietal cortex (Culham and Valyear, 2006) and can be selectively impaired by left parietal injury. However, is this capacity a specifically human adaptation? A monkey model of tool use has been developed by Iriki and collaborators (Iriki, 2005). Training to use a rake enhances activation in anterior intraparietal cortex contralateral to the trained hand, at a location plausibly homologous to the one identified in human fMRI studies. Tool use training leads to a shift in parietal neuron's spatial receptive fields, an induction of expression of immediate-early and neurotrophic factor genes, and even a growth of new connections to distant cortical areas. Thus, a brain area with the capacity to be recycled for tool use may already be present in the monkey, although it appears probable that it is specifically enhanced in the human brain (Orban et al., 2006).

Other Anthropological Domains

We share with anthropologist Dan Sperber the view that a large number of other classical domains of anthropological study, such as music, art, religion, or parental structure, are likely to ultimately fall to a neuronal recycling interpretation, although the relevant brain systems or ''modules'' remain to be solidly identified (Sperber and Hirschfeld, 2004). For instance, Sperber and Hirschfeld discuss the culturally universal propensity for facial manipulation (using masks, cosmetics, caricature, scarification, etc.) as possibly arising from the nature of face coding in the human brain, which allows these cultural artifacts to function as ''super-stimuli'' for the fusiform face area. Similarly, the origins of music may lie in a human-specific, top-down manipulation of pre-existing representations of pitch, rhythm, and timbre (for an overview, see Wallin et al., 2000).

Conclusion

Although much progress has been made in understanding the origins of some key domains of human culture, we conclude by noting that the present paper leaves untouched one important issue with which we started: if precursors of human cultural abilities are present in nonhuman primates, why are we the only species to develop full-blown culture? A significantly prolonged period of brain growth and plasticity (Coqueugniot et al., 2004), a specifically human capacity for cultural transmission and pedagogy, perhaps due to a new talent for representing what others know (Tomasello, 2000), as well as an enhanced capacity for long-range cortico-cortical communication and top-down recruitment of specific brain processors via a ''global neuronal workspace,'' particularly involving prefrontal cortex (Dehaene and Naccache, 2001; Elston, 2003; Mithen, 1996), may all have contributed to the innovative exploitation of the cultural niche by *Homo sapiens*.

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REFERENCES

Allison, T., McCarthy, G., Nobre, A.C., Puce, A., and Belger, A. (1994). Human extrastriate visual cortex and the perception of faces, words, numbers and colors. Cereb. Cortex *5*, 544–554.

Ansari, D., and Dhital, B. (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: an event-related functional magnetic resonance imaging study. J. Cogn. Neurosci. *18*, 1820–1828.

Baker, C.I., Liu, J., Wald, L.L., Kwong, K.K., Benner, T., and Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. Proc. Natl. Acad. Sci. USA *104*, 9087–9092.

Barkow, J.H., Cosmides, L., and Tooby, J., eds. (1992). The Adapted Mind: Evolutionary Psychology and the Generation of Culture (New York: Oxford University Press).

Barnea-Goraly, N., Eliez, S., Menon, V., Bammer, R., and Reiss, A.L. (2005). Arithmetic ability and parietal alterations: a diffusion tensor imaging study in velocardiofacial syndrome. Brain Res. Cogn. Brain Res. *25*, 735–740.

Ben-Shachar, M., Dougherty, R.F., Deutsch, G.K., and Wandell, B.A. (2007). Differential sensitivity to words and shapes in ventral occipito-temporal cortex. Cereb. Cortex *17*, 1604–1611.

Berger, A., Tzur, G., and Posner, M.I. (2006). Infant brains detect arithmetic errors. Proc. Natl. Acad. Sci. USA *103*, 12649–12653.

Biederman, I. (1987). Recognition-by-components: a theory of human image understanding. Psychol. Rev. *94*, 115–147.

Binder, J.R., Frost, J.A., Hammeke, T.A., Bellgowan, P.S., Springer, J.A., Kaufman, J.N., and Possing, E.T. (2000). Human temporal lobe activation by speech and nonspeech sounds. Cereb. Cortex *10*, 512–528.

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.

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.

Booth, M.C., and Rolls, E.T. (1998). View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. Cereb. Cortex *8*, 510–523.

Bremmer, F., Schlack, A., Shah, N.J., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., and Fink, G.R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. Neuron *29*, 287–296.

Brincat, S.L., and Connor, C.E. (2004). Underlying principles of visual shape selectivity in posterior inferotemporal cortex. Nat. Neurosci. *7*, 880–886.

Cai, Q., Lavidor, M., Brysbaert, M., Paulignan, Y., and Nazir, T. (2007). Cerebral lateralization of frontal lobe language processes and lateralization of the posterior visual word processing system. J. Cogn. Neurosci., in press.

Cantlon, J.F., Brannon, E.M., Carter, E.J., and Pelphrey, K.A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. PLoS Biol. *4*, e125. 10.1371/journal.pbio.0040125.

Castelli, F., Glaser, D.E., and Butterworth, B. (2006). Discrete and analogue quantity processing in the parietal lobe: a functional MRI study. Proc. Natl. Acad. Sci. USA *103*, 4693–4698.

Changizi, M.A., and Shimojo, S. (2005). Character complexity and redundancy in writing systems over human history. Proc Biol. Sci *272*, 267–275.

Changizi, M.A., Zhang, Q., Ye, H., and Shimojo, S. (2006). The structures of letters and symbols throughout human history are selected to match those found in objects in natural scenes. Am. Nat. *167*, E117–E139.

Chochon, F., Cohen, L., van de Moortele, P.F., and Dehaene, S. (1999). Differential contributions of the left and right inferior parietal lobules to number processing. J. Cogn. Neurosci. *11*, 617–630.

Christiansen, M.H., and Kirby, S. (2003). Language Evolution (New York: Oxford University Press).

Cohen, L., and Dehaene, S. (2004). Specialization within the ventral stream: the case for the visual word form area. Neuroimage *22*, 466–476.

Cohen Kadosh, R., and Henik, A. (2006). A common representation for semantic and physical properties: a cognitive-anatomical approach. Exp. Psychol. *53*, 87–94.

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.

Cohen, L., Lehericy, 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.

Cohen, L., Martinaud, O., Lemer, C., Lehéricy, S., Samson, Y., Obadia, M., Slachevsky, A., and Dehaene, S. (2003). Visual word recognition in the left and right hemispheres: Anatomical and functional correlates of peripheral alexias. Cereb. Cortex *13*, 1313–1333.

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.

Coqueugniot, H., Hublin, J.J., Veillon, F., Houet, F., and Jacob, T. (2004). Early brain growth in Homo erectus and implications for cognitive ability. Nature *431*, 299–302.

Culham, J.C., and Valyear, K.F. (2006). Human parietal cortex in action. Curr. Opin. Neurobiol. *16*, 205–212.

Culham, J.C., Cavina-Pratesi, C., and Singhal, A. (2006). The role of parietal cortex in visuomotor control: what have we learned from neuroimaging? Neuropsychologia *44*, 2668–2684.

Danziger, E., and Pederson, E. (1998). Through the looking glass: Literacy, writing systems and mirror-image discrimination. Written Language and Literacy *1*, 153–167.

Dehaene, S. (2005). Evolution of human cortical circuits for reading and arithmetic: The "neuronal recycling" hypothesis. In From Monkey Brain to Human Brain, S. Dehaene, J.R. Duhamel, M. Hauser, and G. Rizzolatti, eds. (Cambridge, MA: MIT Press), pp. 133–157.

Dehaene, S. (2007a). Les neurones de la lecture (Paris: Odile Jacob) (English translation: Reading in the brain. New York, Penguin, to appear in 2008).

Dehaene, S. (2007b). Symbols and quantities in parietal cortex: Elements of a mathematical theory of number representation and manipulation. In Attention & Performance XXII. Sensori-motor foundations of higher cognition, P. Haggard and Y. Rossetti, eds. (Cambridge, MA: Harvard University Press), in press.

Dehaene, S., and Changeux, J.P. (1993). Development of elementary numerical abilities: A neuronal model. J. Cogn. Neurosci. *5*, 390–407.

Dehaene, S., and Cohen, L. (1995). Towards an anatomical and functional model of number processing. Math. Cogn. *1*, 83–120.

Dehaene, S., and Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. Cognition *79*, 1–37.

Dehaene, S., Tzourio, N., Frak, V., Raynaud, L., Cohen, L., Mehler, J., and Mazoyer, B. (1996). Cerebral activations during number multiplication and comparison: a PET study. Neuropsychologia *34*, 1097–1106.

Dehaene, S., Dupoux, E., Mehler, J., Cohen, L., Paulesu, E., Perani, D., van de Moortele, P.F., Lehéricy, S., and Le Bihan, D. (1997). Anatomical variability in the cortical representation of first and second languages. Neuroreport *8*, 3809–3815.

Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., and Tsivkin, S. (1999). Sources of mathematical thinking: behavioral and brain-imaging evidence. Science *284*, 970–974.

Dehaene, S., Naccache, L., Cohen, L., Bihan, D.L., Mangin, J.F., Poline, J.B., and Riviere, D. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. Nat. Neurosci. *4*, 752–758.

Dehaene, S., Le Clec'H, G., Poline, J.B., Le Bihan, D., and Cohen, L. (2002). The visual word form area: a prelexical representation of visual words in the fusiform gyrus. Neuroreport *13*, 321–325.

Dehaene, S., Piazza, M., Pinel, P., and Cohen, L. (2003). Three parietal circuits for number processing. Cogn. Neuropsychol. *20*, 487–506.

Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J.B., Le Bihan, D., and Cohen, L. (2004). Letter binding and invariant recognition of masked words: behavioral and neuroimaging evidence. Psychol. Sci. *15*, 307–313.

Dehaene, S., Cohen, L., Sigman, M., and Vinckier, F. (2005). The neural code for written words: a proposal. Trends Cogn. Sci. *9*, 335–341.

Dehaene-Lambertz, G., Dehaene, S., Anton, J.L., Campagne, A., Ciuciu, P., Dehaene, G.P., Denghien, I., Jobert, A., Lebihan, D., Sigman, M., et al. (2006a). Functional segregation of cortical language areas by sentence repetition. Hum. Brain Mapp. *27*, 360–371.

Dehaene-Lambertz, G., Hertz-Pannier, L., Dubois, J., Meriaux, S., Roche, A., Sigman, M., and Dehaene, S. (2006b). Functional organization of perisylvian activation during presentation of sentences in preverbal infants. Proc. Natl. Acad. Sci. USA *103*, 14240–14245.

Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., and Benke, T. (2003). Learning complex arithmetic–an fMRI study. Brain Res. Cogn. Brain Res. *18*, 76–88.

Diester, I., and Nieder, A. (2007). Semantic associations between signs and numerical categories in the prefrontal cortex. PLoS Biol., in press.

Ding, G., Peng, D., and Taft, M. (2004). The nature of the mental representation of radicals in Chinese: a priming study. J. Exp. Psychol. Learn. Mem. Cogn. *30*, 530–539.

Duhamel, J.R., Colby, C.L., and Goldberg, M.E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. Science *255*, 90–92.

Eger, E., Sterzer, P., Russ, M.O., Giraud, A.L., and Kleinschmidt, A. (2003). A supramodal number representation in human intraparietal cortex. Neuron *37*, 719–725.

Eliez, S., Blasey, C.M., Menon, V., White, C.D., Schmitt, J.E., and Reiss, A.L. (2001). Functional brain imaging study of mathematical reasoning abilities in velocardiofacial syndrome (del22q11.2). Genet. Med. *3*, 49–55.

Elston, G.N. (2003). Cortex, cognition and the cell: new insights into the pyramidal neuron and prefrontal function. Cereb. Cortex *13*, 1124–1138.

Feigenson, L., Dehaene, S., and Spelke, E. (2004). Core systems of number. Trends Cogn. Sci. *8*, 307–314.

Fias, W., Lammertyn, J., Reynvoet, B., Dupont, P., and Orban, G.A. (2003). Parietal representation of symbolic and nonsymbolic magnitude. J. Cogn. Neurosci. *15*, 47–56.

Flombaum, J.I., Junge, J.A., and Hauser, M.D. (2005). Rhesus monkeys (Macaca mulatta) spontaneously compute addition operations over large numbers. Cognition *97*, 315–325.

Formisano, E., Kim, D.S., Di Salle, F., van de Moortele, P.F., Ugurbil, K., and Goebel, R. (2003). Mirror-symmetric tonotopic maps in human primary auditory cortex. Neuron *40*, 859–869.

Fritz, J., Mishkin, M., and Saunders, R.C. (2005). In search of an auditory engram. Proc. Natl. Acad. Sci. USA *102*, 9359–9364.

Gaillard, R., Naccache, L., Pinel, P., Clemenceau, S., Volle, E., Hasboun, D., Dupont, S., Baulac, M., Dehaene, S., Adam, C., and Cohen, L. (2006). Direct intracranial, FMRI, and lesion evidence for the causal role of left inferotemporal cortex in reading. Neuron *50*, 191–204.

Ghazanfar, A.A., and Hauser, M.D. (1999). The neuroethology of primate vocal communication: substrates for the evolution of speech. Trends Cogn. Sci. *3*, 377–384.

Gilbert, C.D., Sigman, M., and Crist, R.E. (2001). The neural basis of perceptual learning. Neuron *31*, 681–697.

Gilmore, C.K., McCarthy, S.E., and Spelke, E.S. (2007). Symbolic arithmetic knowledge without instruction. Nature *447*, 589–591.

Goldman-Rakic, P.S., and Schwartz, M.L. (1982). Interdigitation of contralateral and ipsilateral columnar projections to frontal association cortex. Science *216*, 755–757.

Gould, S.J., and Vrba, E.S. (1982). Exaptation: A missing term in the science of form. Paleobiology *8*, 4–15.

Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzchak, Y., and Malach, R. (1998). A sequence of object-processing stages revealed by fMRI in the human occipital lobe. Hum. Brain Mapp. *6*, 316–328.

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.

Hasson, U., Harel, M., Levy, I., and Malach, R. (2003). Large-scale mirror-symmetry organization of human occipito-temporal object areas. Neuron *37*, 1027–1041.

Horton, J.C., and Adams, D.L. (2005). The cortical column: a structure without a function. Philos. Trans. R. Soc. Lond. B Biol. Sci. *360*, 837–862.

Hubbard, E.M., Piazza, M., Pinel, P., and Dehaene, S. (2005). Interactions between number and space in parietal cortex. Nat. Rev. Neurosci. *6*, 435–448.

Humphries, C., Binder, J.R., Medler, D.A., and Liebenthal, E. (2006). Syntactic and semantic modulation of neural activity during auditory sentence comprehension. J. Cogn. Neurosci. *18*, 665–679.

Iriki, A. (2005). A prototype of Homo-Faber: A silent precursor of human intelligence in the tool-using monkey brain. In From Monkey Brain to Human Brain, S. Dehaene, J.R. Duhamel, M. Hauser, and G. Rizzolatti, eds. (Cambridge, MA: MIT Press), pp. 133–157.

Isaacs, E.B., Edmonds, C.J., Lucas, A., and Gadian, D.G. (2001). Calculation difficulties in children of very low birthweight: A neural correlate. Brain *124*, 1701–1707.

Ischebeck, A., Zamarian, L., Siedentopf, C., Koppelstatter, F., Benke, T., Felber, S., and Delazer, M. (2006). How specifically do we learn? Imaging the learning of multiplication and subtraction. Neuroimage *30*, 1365–1375.

Ishai, A., Ungerleider, L.G., Martin, A., Schouten, J.L., and Haxby, J.V. (1999). Distributed representation of objects in the human ventral visual pathway. Proc. Natl. Acad. Sci. USA *96*, 9379–9384.

Jobard, G., Crivello, F., and Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. Neuroimage *20*, 693–712.

Kaas, J.H., and Hackett, T.A. (2000). Subdivisions of auditory cortex and processing streams in primates. Proc. Natl. Acad. Sci. USA *97*, 11793–11799.

Kayaert, G., Biederman, I., and Vogels, R. (2005). Representation of regular and irregular shapes in macaque inferotemporal cortex. Cereb. Cortex *15*, 1308–1321.

Kitterle, F.L., and Selig, L.M. (1991). Visual field effects in the discrimination of sine-wave gratings. Percept. Psychophys. *50*, 15–18.

Krubitzer, L., and Kahn, D.M. (2003). Nature versus nurture revisited: an old idea with a new twist. Prog. Neurobiol. *70*, 33–52.

Kucian, K., Loenneker, T., Dietrich, T., Dosch, M., Martin, E., and von Aster, M. (2006). Impaired neural networks for approximate calculation in dyscalculic children: a functional MRI study. Behav. Brain Funct. *2*, 31.

Lachmann, T., and van Leeuwen, C. (2007). Paradoxical enhancement of letter recognition in developmental dyslexia. Dev. Neuropsychol. *31*, 61–77.

Lee, K.M. (2000). Cortical areas differentially involved in multiplication and subtraction: A functional magnetic resonance imaging study and correlation with a case of selective acalculia. Ann. Neurol. *48*, 657–661.

Lee, C.Y., Tsai, J.L., Kuo, W.J., Yeh, T.C., Wu, Y.T., Ho, L.T., Hung, D.L., Tzeng, O.J., and Hsieh, J.C. (2004). Neuronal correlates of consistency and frequency effects on Chinese character naming: an event-related fMRI study. Neuroimage *23*, 1235–1245.

Lerner, Y., Hendler, T., Ben-Bashat, D., Harel, M., and Malach, R. (2001). A hierarchical axis of object processing stages in the human visual cortex. Cereb. Cortex *11*, 287–297.

Levy, L.M., Reis, I.L., and Grafman, J. (1999). Metabolic abnormalities detected by H-MRS in dyscalculia and dysgraphia. Neurology *53*, 639–641.

Malach, R., Levy, I., and Hasson, U. (2002). The topography of high-order human object areas. Trends Cogn. Sci. *6*, 176–184.

Maurer, U., Brem, S., Kranz, F., Bucher, K., Benz, R., Halder, P., Steinhausen, H.C., and Brandeis, D. (2006). Coarse neural tuning for print peaks when children learn to read. Neuroimage *33*, 749–758.

Mazoyer, B.M., Dehaene, S., Tzourio, N., Frak, V., Syrota, A., Murayama, N., Levrier, O., Salamon, G., Cohen, L., and Mehler, J. (1993). The cortical representation of speech. J. Cogn. Neurosci. *5*, 467–479.

Medendorp, W.P., Goltz, H.C., Vilis, T., and Crawford, J.D. (2003). Gaze-centered updating of visual space in human parietal cortex. J. Neurosci. *23*, 6209–6214.

Mithen, S. (1996). The Prehistory of the Mind: The Cognitive Origins of Art, Religion and Science (London: Thames & Hudson).

Molko, N., Cachia, A., Riviere, D., Mangin, J.F., Bruandet, M., Le Bihan, D., Cohen, L., and Dehaene, S. (2003). Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. Neuron *40*, 847–858.

Morais, J., and Kolinsky, R. (2005). Literacy and cognitive change. In The Science of Reading, A. Handbook, M. Snowling and C. Hulme, eds. (Oxford: Blackwell), pp. 188–203.

Naccache, L., and Dehaene, S. (2001). The Priming method: Imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. Cereb. Cortex *11*, 966–974.

Nakamura, K., Dehaene, S., Jobert, A., Le Bihan, D., and Kouider, S. (2005). Subliminal convergence of Kanji and Kana words: further evidence for functional parcellation of the posterior temporal cortex in visual word perception. J. Cogn. Neurosci. *17*, 954–968.

Nieder, A., and Miller, E.K. (2003). Coding of cognitive magnitude. Compressed scaling of numerical information in the primate prefrontal cortex. Neuron *37*, 149–157.

Nieder, A., and Miller, E.K. (2004). A parieto-frontal network for visual numerical information in the monkey. Proc. Natl. Acad. Sci. USA *101*, 7457–7462.

Nieder, A., and Merten, K. (2007). A labeled-line code for small and large numerosities in the monkey prefrontal cortex. J. Neurosci., in press.

Nieder, A., Freedman, D.J., and Miller, E.K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. Science *297*, 1708–1711.

Nieder, A., Diester, I., and Tudusciuc, O. (2006). Temporal and spatial enumeration processes in the primate parietal cortex. Science *313*, 1431–1435.

Orban, G.A., Claeys, K., Nelissen, K., Smans, R., Sunaert, S., Todd, J.T., Wardak, C., Durand, J.B., and Vanduffel, W. (2006). Mapping the parietal cortex of human and non-human primates. Neuropsychologia *44*, 2647–2667.

Pallier, C., Dehaene, S., Poline, J.B., LeBihan, D., Argenti, A.M., Dupoux, E., and Mehler, J. (2003). Brain imaging of language plasticity in adopted adults: can a second language replace the first? Cereb. Cortex *13*, 155–161.

Pandya, D.N., and Yeterian, E.H. (1990). Architecture and connections of cerebral cortex: implications for brain evolution and function. In Neurobiology of Higher Cognitive Functions, A.B. Scheibel and A.F. Wechsler, eds. (New York: The Guilford Press), pp. 53–84.

Paulesu, E., McCrory, E., Fazio, F., Menoncello, L., Brunswick, N., Cappa, S.F., Cotelli, M., Cossu, G., Corte, F., Lorusso, M., et al. (2000). A cultural effect on brain function. Nat. Neurosci. *3*, 91–96.

Petersen, S.E., Fox, P.T., Posner, M.I., Mintun, M., and Raichle, M.E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. Nature *331*, 585–589.

Philipose, L.E., Gottesman, R.F., Newhart, M., Kleinman, J.T., Herskovits, E.H., Pawlak, M.A., Marsh, E.B., Davis, C., Heidler-Gary, J., and Hillis, A.E. (2007). Neural regions essential for reading and spelling of words and pseudowords. Ann. Neurol., in press. Published online August 13, 2007. 10.1002/ana.21182.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., and Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. Neuron *44*, 547–555.

Piazza, M., Mechelli, A., Price, C.J., and Butterworth, B. (2006). Exact and approximate judgements of visual and auditory numerosity: an fMRI study. Brain Res. *1106*, 177–188.

Piazza, M., Pinel, P., Le Bihan, D., and Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. Neuron *53*, 293–305.

Pica, P., Lemer, C., Izard, V., and Dehaene, S. (2004). Exact and approximate arithmetic in an Amazonian indigene group. Science *306*, 499–503.

Pinel, P., Dehaene, S., Riviere, D., and LeBihan, D. (2001). Modulation of parietal activation by semantic distance in a number comparison task. Neuroimage *14*, 1013–1026.

Pinel, P., Piazza, M., Le Bihan, D., and Dehaene, S. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. Neuron *41*, 983–993.

Pinker, S. (2002). The Blank Slate: The Modern Denial of Human Nature (London: Penguin books).

Poremba, A., Malloy, M., Saunders, R.C., Carson, R.E., Herscovitch, P., and Mishkin, M. (2004). Species-specific calls evoke asymmetric activity in the monkey's temporal poles. Nature *427*, 448–451.

Puce, A., Allison, T., Asgari, M., Gore, J.C., and McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. J. Neurosci. *16*, 5205–5215.

Quartz, S.R., and Sejnowski, T.J. (1997). The neural basis of cognitive development: a constructivist manifesto. Behav. Brain Sci. *20*, 537–556.

Quiroga, R.Q., Reddy, L., Kreiman, G., Koch, C., and Fried, I. (2005). Invariant visual representation by single neurons in the human brain. Nature *435*, 1102–1107.

Rivera, S.M., Reiss, A.L., Eckert, M.A., and Menon, V. (2005). Developmental changes in mental arithmetic: Evidence for increased functional specialization in the left inferior parietal cortex. Cereb. Cortex *15*, 1779–1790.

Roitman, J.D., Brannon, E.M., and Platt, M.L. (2007). Monotonic coding of numerosity in macaque lateral intraparietal area. PLoS Biol. *5*, e208. 10.1371/journal.pbio.0050208.

Roland, P.E., and Friberg, L. (1985). Localization of cortical areas activated by thinking. J. Neurophysiol. *53*, 1219–1243.

Rollenhagen, J.E., and Olson, C.R. (2000). Mirror-image confusion in single neurons of the macaque inferotemporal cortex. Science *287*, 1506–1508.

Rolls, E.T. (2000). Functions of the primate temporal lobe cortical visual areas in invariant visual object and face recognition. Neuron *27*, 205–218.

Rueckert, L., Lange, N., Partiot, A., Appollonio, I., Litvar, I., Le Bihan, D., and Grafman, J. (1996). Visualizing cortical activation during mental calculation with functional MRI. NeuroImage *3*, 97–103.

Sawamura, H., Shima, K., and Tanji, J. (2002). Numerical representation for action in the parietal cortex of the monkey. Nature *415*, 918–922.

Schlaggar, B.L., and McCandliss, B.D. (2007). Development of neural systems for reading. Annu. Rev. Neurosci. *30*, 475–503.

Sereno, M.I., and Huang, R.S. (2006). A human parietal face area contains aligned head-centered visual and tactile maps. Nat. Neurosci. *9*, 1337–1343.

Serre, T., Oliva, A., and Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. Proc. Natl. Acad. Sci. USA *104*, 6424–6429.

Shaywitz, B.A., Shaywitz, S.E., Pugh, K.R., Mencl, W.E., Fulbright, R.K., Skudlarski, P., Constable, R.T., Marchione, K.E., Fletcher, J.M., Lyon, G.R., and Gore, J.C. (2002). Disruption of posterior brain systems for reading in children with developmental dyslexia. Biol. Psychiatry *52*, 101–110.

Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., and Dehaene, S. (2002). Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. Neuron *33*, 475–487.

Simon, O., Kherif, F., Flandin, G., Poline, J.B., Riviere, D., Mangin, J.F., Le Bihan, D., and Dehaene, S. (2004). Automatized clustering and functional geometry of human parietofrontal networks for language, space, and number. Neuroimage *23*, 1192–1202.

Sperber, D., and Hirschfeld, L.A. (2004). The cognitive foundations of cultural stability and diversity. Trends Cogn. Sci. *8*, 40–46.

Tanaka, K. (2003). Columns for complex visual object features in the inferotemporal cortex: clustering of cells with similar but slightly different stimulus selectivities. Cereb. Cortex *13*, 90–99.

Tang, Y., Zhang, W., Chen, K., Feng, S., Ji, Y., Shen, J., Reiman, E.M., and Liu, Y. (2006). Arithmetic processing in the brain shaped by cultures. Proc. Natl. Acad. Sci. USA *103*, 10775–10780.

Temple, E., and Posner, M.I. (1998). Brain mechanisms of quantity are similar in 5-year-olds and adults. Proc. Natl. Acad. Sci. USA *95*, 7836–7841.

Tomasello, M. (2000). The Cultural Origins of Human Cognition (Cambridge, MA: Harvard University Press).

Tudusciuc, O., and Nieder, A. (2007). Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. Proc. Natl. Acad. Sci. USA *104*, 14513–14518.

Turing, A.M. (1952). The chemical basis of morphogenesis. Philos. Trans. R. Soc. Lond. B Biol. Sci. *237*, 37–72.

Turkeltaub, P.E., Gareau, L., Flowers, D.L., Zeffiro, T.A., and Eden, G.F. (2003). Development of neural mechanisms for reading. Nat. Neurosci. *6*, 767–773.

Venkatraman, V., Siong, S.C., Chee, M.W., and Ansari, D. (2006). Effect of language switching on arithmetic: a bilingual FMRI study. J. Cogn. Neurosci. *18*, 64–74.

Verguts, T., and Fias, W. (2004). Representation of number in animals and humans: a neural model. J. Cogn. Neurosci. *16*, 1493–1504.

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.

Wallin, N.L., Merker, B., and Brown, S. (2000). The Origins of Music (Cambridge, MA: MIT Press).

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E., Wrangham, R.W., and Boesch, C. (1999). Cultures in chimpanzees. Nature *399*, 682–685.

Yacoub, E., Shmuel, A., Logothetis, N., and Ugurbil, K. (2007). Robust detection of ocular dominance columns in humans using Hahn Spin Echo BOLD functional MRI at 7 Tesla. Neuroimage *37*, 1161–1177.

Ziegler, J.C., and Goswami, U. (2005). Reading acquisition, developmental dyslexia, and skilled reading across languages: a psycholinguistic grain size theory. Psychol. Bull. *131*, 3–29.