The neural code for written words: a proposal

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How is reading, a cultural invention, coded by neural populations in the human brain? The neural code for written words must be abstract, because we can recognize words regardless of their location, font and size. Yet it must also be exquisitely sensitive to letter identity and letter order. Most existing coding schemes are insufficiently invariant or incompatible with the constraints of the visual system. We propose a tentative neuronal model according to which part of the occipito-temporal 'what' pathway is tuned to writing and forms a hierarchy of local combination detectors sensitive to increasingly larger fragments of words. Our proposal can explain why the detection of 'open bigrams' (ordered pairs of letters) constitutes an important stage in visual word recognition.

The problem of the neural code for words

Visual word recognition is a remarkable feat. Within a fraction of a second, a pattern of light on the retina is recognized as a word, invariantly over changes in ^{position}, size, CASE and *font*. This invariance implies neglecting large differences in visual form (e.g. between 'A' and 'a'), while attending to small details such as the distinction between 'e' and 'c'. The spatial arrangement of letters must also be maintained, to separate 'dog' from 'god', for example. Finally, these constraints vary across scripts. For instance, English readers might not notice the difference between ת and ה, but it defines two distinct letters in Hebrew.

It is extremely unlikely that the brain contains in-built mechanisms designed for reading, a recent cultural invention (<5400 years). Thus, learning to read must involve a pre-emption of part of the existing visual system and its conversion, by minimal modification, to process the shapes of letters and words. Indeed, in most expert readers, a localized region of the left occipito-temporal sulcus, just lateral to the fusiform gyrus, systematically takes on the function of identifying visual letter strings. This 'visual word form system' [1,2] is thought to play a pivotal role in informing other temporal, parietal and frontal areas of the identity of the letter string, for the purpose of both semantic access and phonological retrieval. Thus, it must provide a compact 'neural code'

for visual words, a cell assembly unique to each word, yet invariant under changes in location, size, case and font.

Cracking the code for written words: the 'open bigrams' proposal

Cracking the cerebral code for written words has become an active topic of experimental [3–7] and theoretical [8,9] investigations. Although many connectionist models of reading have been proposed, most have focused on the interactions between orthography, phonology and semantics, ignoring the 'front end' of visual word recognition. As a result, these models often presuppose a case- and location-invariant representation (see Box 1).

Recently, however, Grainger and Whitney described a promising scheme called 'open bigrams' [7–9]. In this

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Box 1. Main coding schemes used in connectionist models of reading

How are visual inputs coded in connectionist models of reading? A classical scheme, called 'slot-coding', used in most models [35–40], consists in a spatial array of case-independent letter detectors. An entire bank of units coding for every possible letter is replicated at each location or 'slot'. Thus, the word *CAN* is represented by activating unit *C* in slot 1, unit *A* in slot 2, and unit *N* in slot 3.

Although this scheme is simple, it bypasses entirely the issue of location and case invariance: the inputs are merely supposed to be case-independent and spatially justified. Indeed, the code is radically changed whenever a word is shifted by one letter location. Although various alignment schemes have been proposed – alignment on the first letter [40], the preferred viewing position [38], or the first vowel [37], possibly with syllabic structuring of consonants into onset and coda [39]–, all suffer from a lack of generalization across locations. As a consequence, most slot-coding schemes provide no explanation for the known similarity of words with transposed letters (e.g. *ANSWER–ANWSER*), shared letter sequences (e.g. *LEGAL–GALA*), or morphemes (e.g. *REPLAY–PLAY*) if they are misaligned [3].

The need to encode relative rather than absolute letter location led to the invention of 'wickelcoding', where a word is encoded by its triplets of letters [17,41–43]. For instance, the word *TICS* is encoded by units sensitive to the substrings *#TI*, *TIC*, *ICS* and *CS#* (where *#* represents the space between words. However, wickelcoding fails to account for the similarity metric of visual words. For instance, the words *COP* and *CAP* are coded by entirely different units. The problem can be mitigated by using more flexible wickelcodes, for instance one in which a unit is dedicated to the sequence *C_P*, where _ stands for any intermediate letter [17]. Again, however, this code is merely stipulated to be case-invariant and location-invariant. Only a single model [17], which bears significant similarity to the present LCD model, included a hierarchical processing stream capable of extracting a location-invariant Wickelcode from a simulated retinal input, although no solution was proposed for case-invariance.

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Box 2. Essential properties of primate visual cortex that may be relevant for word recognition

Much is known about the organization of the ventral occipito-temporal route for object recognition, in both humans [44] and macaques [10,11]. Here, we briefly summarize the key properties that are likely to be relevant to reading.

Hierarchical organization

The ventral visual pathway is organized as a hierarchy of areas connected by both feedforward and feedback pathways (see Figure I). From posterior occipital to more anterior inferotemporal regions, the size of the neurons' receptive fields increases by a factor of 2–3. This is accompanied by a systematic increase in the complexity of the neurons' preferred features, from line segments to whole objects, and a corresponding increase in invariance for illumination, size, or location.

Shape selectivity

Columns of neurons in inferotemporal form a broad repertoire of shape primitives, including simple letter-like shapes such as T or L, which are collectively capable of representing many objects. [45]. Their selectivity is thought to arise from the neurons' capacity to integrate, in a spatially specific manner, inputs from multiple, hierarchically lower neurons, each selective to more elementary view or contour elements

[46]. This mechanism is also thought to contribute to spatial invariance, through pooling of multiple local detectors [10,11].

Plasticity and perceptual learning

Inferotemporal neurons are plastic and, through training, can become attuned to any image [34,47]. A single neuron may also become responsive to several arbitrary images that are repeatedly presented in temporal association [48]. This mechanism might play a role in the acquisition of multiple representations of the same letters (e.g. upper- and lower-case).

Large-scale visual biases

fMRI has revealed that the human occipito-temporal region is traversed by a large-scale gradient of excentricity bias [44], with lateral regions being more responsive to small foveal objects, and mesial regions to the periphery of the visual field. Written words and faces, which are both visually detailed and require foveation, tend to lie within foveally biased visual cortex. [44] Retinotopic gradients, together with hemispheric asymmetries in downstream language areas, might help explain why word recognition involves a reproducible left inferotemporal region in all individuals.
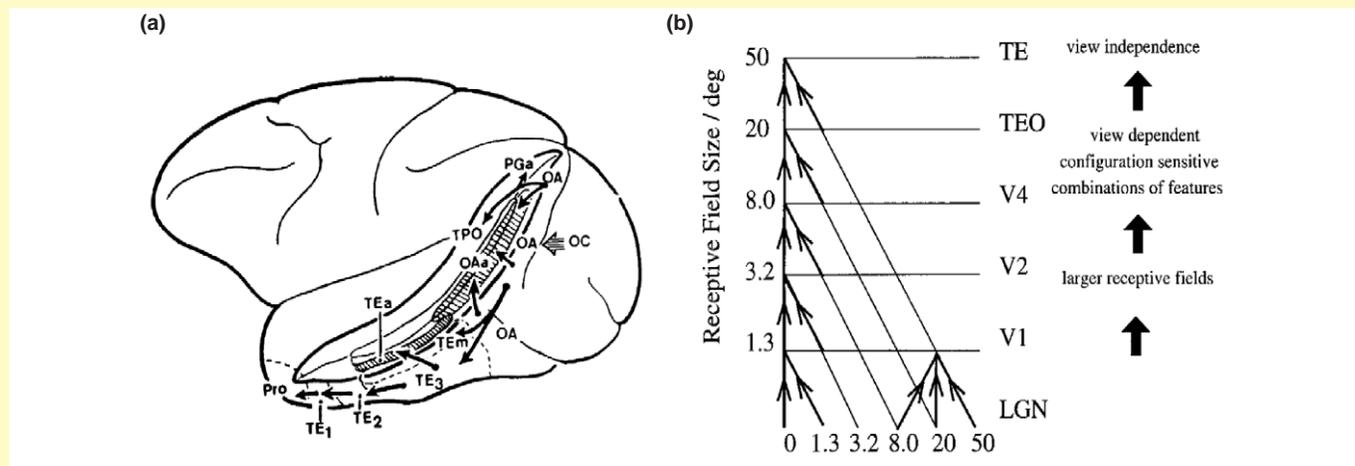

Figure I. Schematic organization of the macaque occipito-temporal pathway for visual recognition. (a) Information processing progresses from primary visual cortex (area OC) to prestriate cortex (OA) and then ventrally to multiple cytoarchitectonicaly defined areas of inferior temporal cortex (TE) and temporal polar pro-isocortex (area Pro). Connections towards inferior parietal cortex (PG) and the temporo-parieto-occipital junction (TPO) are also shown. Although the dorsal system is also likely to contribute to reading, particularly for unfamiliar words and when multiple serial fixations are needed, this contribution is not considered here for lack of space. (b) This diagram emphasizes a hierarchical feedforward scheme in which receptive size increases by a factor of 2.5 at each stage, in parallel with an increasing sensitivity to feature combinations and a decreasing sensitivity to location or viewpoint. (Reproduced with permission from [10].)

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scheme, words are coded by the ordered letter pairs that they contain, even when separated by a few intermediate letters. The open bigram detector for EN, for instance, reacts to the presence, anywhere on the retina, of a letter E to the left of a letter N, even if up to two letters are present in between. The word TICS, then, would be coded by the list TI, TC, TS, IC, IS and CS. Grainger and Whitney briefly review how their scheme might account for the known metric of similarity of words, as derived from experimental studies of priming and confusions [8]. One of the key supportive findings for open bigrams is that a word can be primed by a subset of its letters, providing that letter order is preserved (for instance, 'grdn' primes *garden*, but 'gdrn' does not) [4,5].

Nevertheless, one problem is that the open bigram scheme fails to assign a unique code to each word. When words contain repeated letters, several words can have the same set of open bigrams, for instance *losses* and *loses*,

nana and *anna*, *isis* and *sissi*. The open bigram scheme also predicts that many spellings of a given word are equivalent, for example, *sense* versus 'esnes', 'sesnes', 'seesnesee', and so on. Such strings might be confusable, but it is implausible that they are coded as equivalent.

A neurobiological framework for visual word recognition

Most cognitive psychological coding schemes are formal and detached from neuroscience. We suggest that much can be gained by taking advantage of the large amount of information available on the neurophysiology of visual recognition (Box 2). From this biological standpoint, existing models are least realistic in their attempt to achieve location invariance in a single step, by a sudden jump for location-specific letter detectors to larger location-independent units. In reality, as one moves up the visual hierarchy, receptive fields do not suddenly
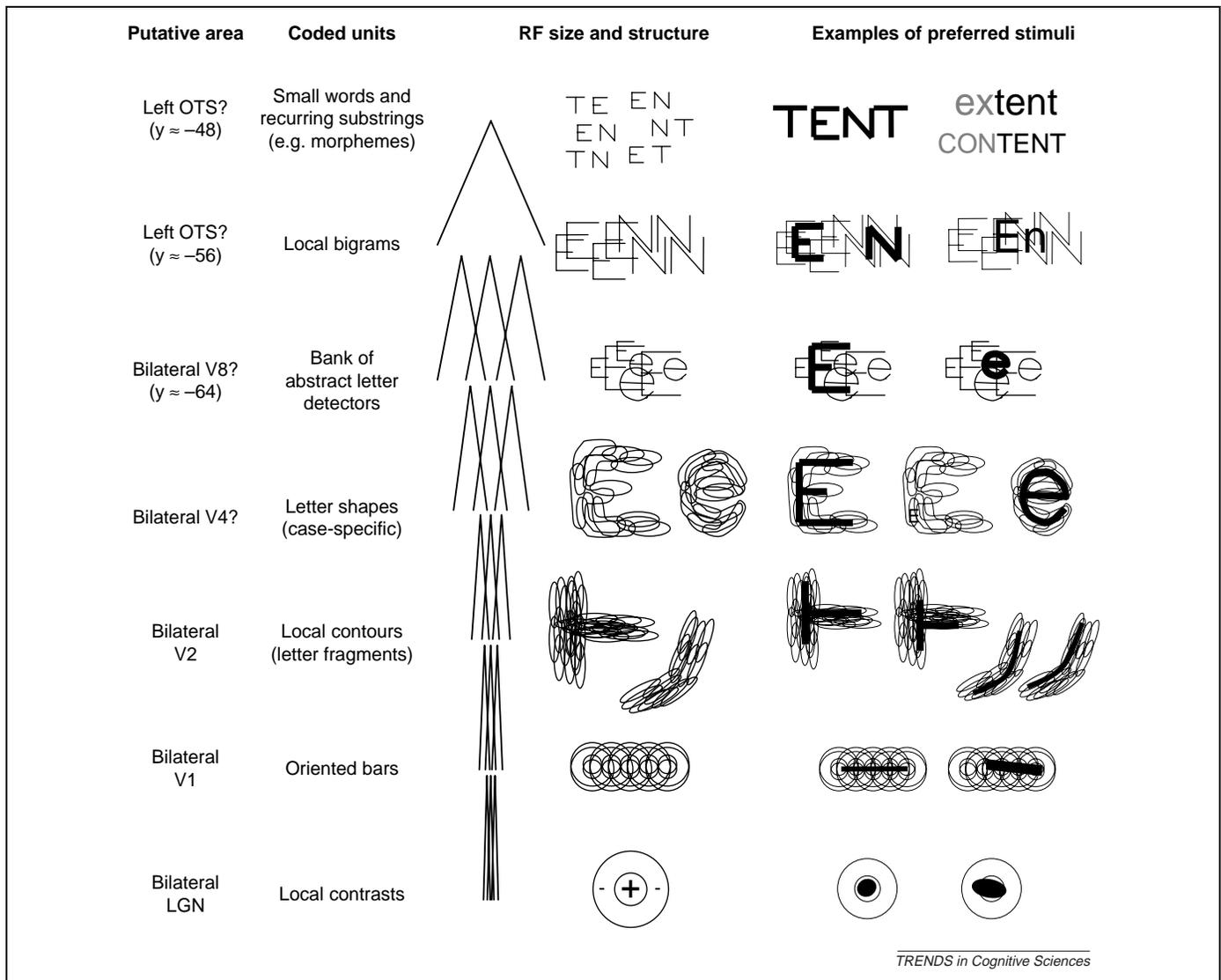
Figure 1. Model of invariant word recognition by a hierarchy of local combination detectors (LCDs). The model is inspired from neurophysiological models of invariant object recognition [10,11]. Each neuron is assumed to pool activity from a subset of neurons at the immediately lower level, thus lead to an increasing complexity, invariance and size of the receptive field at each stage (see text for details). Note that only the excitatory components of the receptive fields are sketched here; however, both feedforward (e.g. center-surround) and lateral inhibition are likely to contribute significantly to define selective responses. The anatomical localizations are highly tentative, based on recent neuroimaging studies of the visual word form system [1,31] and their coincidence with a standardized atlas of visual areas [54]. Abbreviations: OTS, occipito-temporal sulcus; LGN, lateral geniculate nucleus; y, approximate antero-posterior coordinate relative to the human Montreal Neurological Institute template.

encompass the entire visual field, but progressively become larger, by a factor of 2 to 3, in parallel to an increase in the complexity of the neuron's preferred features [10,11].

Figure 1 shows how a neurobiological scheme of increasingly broader and more abstract local combination detectors (LCDs) might achieve invariant word recognition. At the lower level, combinations of local oriented bars can form local shape fragment detectors, which already have some small tolerance over displacements and changes in size. At the next stage, combinations of fragments can then be used to form local shape detectors. These neurons can detect a letter, but only in a given case and shape. Abstract letter identities can be recognized at the next stage, by pooling activation from populations of shape detectors coding for the different upper and lower-case versions of a letter.

Because their receptive fields remain small, such letter detectors have a moderate tolerance for changes in size

and location. Multiple letter detectors have to be replicated at several locations, thus forming the bank of case-invariant letter detectors postulated in many models.

Crucially, the natural subsequent stage is not location-independent bigram units, but neurons sensitive to *local* combinations of letters. One neuron, for instance, might respond optimally to 'N one or two letters left of A, both around 0.5 degree right of fixation'. Given that receptive field size increases by a factor of 2 or 3, neurons at this level might code for short sequences of 1, 2 or 3 letters. However, there is a trade-off here between location invariance, selectivity, and information conveyed. A neuron coding for a triplet of letters can do so only at a specific location. Hence, it conveys very narrow information, useful for only a few words. Conversely, a neuron coding for a single letter at any of three locations is frequently activated but uninformative about relative letter location. Bigram neurons, however, can respond selectively, yet with some tolerance for location of the

component letters. As shown in Figure 1, this can be achieved by pooling over partially overlapping letter detectors, thus allowing neurons responsive to the pair 'NA' to have a broader receptive field than that of their component letter detector neurons for 'N' and 'A'. Thus, within the connectivity constraints of the visual system, bigram coding appears to provide a good compromise between location invariance and letter-order coding, although we cannot exclude an additional contribution of single-letter or trigram detectors.

The receptive field structure of local bigram detectors explains why they act as 'open bigrams'. Because they have to pool activation from several individual letter detectors to achieve partial location invariance, they inevitably tolerate some imprecision in the location of their component letters, thus allowing one or two other intermediate letters to slip in. Thus, our hierarchical receptive-field scheme can explain *why* open bigrams are used in reading, rather than merely stipulating their existence. Furthermore, most of the desirable properties of the open-bigram scheme are preserved. In particular, strings with missing letters, such as '*grdn*', activate neurons that form a subset of the code for the full word *garden*, thus explaining that one can prime the other [4,5]. Likewise, the code is minimally changed when two letters are transposed, thus explaining that '*jugde*' can prime *judge* [7,12].

Contrary to Grainger and Whitney's proposal, however, the postulated bigram neurons do not detect the presence of 'N left of A' anywhere in the visual field, but maintain some location specificity. Thus, we expect a replication of multiple bigram detectors, each capable of detecting 'N left A' within a certain range of locations. Some of these detectors will fire to the presence of 'NA' at the beginning of 'nana', and will not fire when the stimulus is 'anna'. As a result, the LCD scheme can assign a unique and robust code to each word.

After the bigram level, the natural next step is ordered combinations of bigrams. Here, we expect neurons to begin to react to recurring multiletter strings, including morphemes or small words (Figure 1). Note, however, that at any stage, words are never encoded by a single neuron or column, but by a sparse distributed population of partially redundant neurons.

The cortico-cortical connections needed to establish this hierarchical receptive field structure include intrahemispheric short-range connections, but also, for receptive fields straddling the midline, some longer callosal connections. It has been proposed that 'foveal splitting', whereby the left and right halves of a centrally fixated word are initially sent to distinct hemispheres, has important functional consequences for reading. [13] However, beyond V1, callosal projections have the precise structure required to guarantee the continuity of receptive fields across the midline [14] and allow convergence to common visual representations [15]. We believe that these connections minimize the functional impact of the initial foveal split.

For simplicity, we only included feedforward connections in the model. However, feedback and lateral connections are numerous in the visual system, and

probably contribute to shaping the neurons' receptive field, for instance by enforcing probabilistic relations amongst consecutive letters, or by disambiguating letters and bigrams within words (thus explaining the word superiority effect [16]).

Perceptual learning of local combination detectors

It might be feared that the proposed model leads to a combinatorial explosion, because of the increasing number of letter combinations that are encoded as one moves up the cortical hierarchy. However, this increase is compensated by a progressive decrease in the number of encoded locations as receptive field size increases. Furthermore, it is likely that, in the course of learning to read, perceptual learning mechanisms ensure that only frequent, informative letters and combinations are selected to be represented by dedicated neurons [11,17,18]. At the bigram level, for instance, we might expect detectors for EN, which is useful for recognizing many words, but not for ZH, which is almost never used in English. Indeed, the left inferotemporal 'visual word form' area [1], where letter, bigram and string detectors are presumably located, responds much more to real words and pseudowords than to random consonant strings [19].

As a result of eye movement patterns, words usually appear within a restricted horizontal region close to the fovea and mostly within the right hemifield. Perceptual learning mechanisms would be expected to shape the tuning of local detectors only at those retinal locations. This hypothesis is supported by the frequent observation of an advantage for words presented in the right visual field, within a few degrees of fixation, and in a standard horizontal orientation [20–22].

Perceptual learning should select local detectors for any useful recurrent combination of curves within the cell's receptive field. Thus, in readers of Chinese, neurons might become attuned to entire characters as well as to recurrent combinations within the characters, such as semantic and phonetic radicals [23]. Even in alphabetic scripts, although letters and bigrams are natural units, it is also possible that other regularities would be picked up, such as the 'shape' formed at the junction between two frequent consecutive letters. The detection of cross-letter regularities might be crucial for learning to read handwriting, where letter segmentation is not trivial and might be the outcome of recognition rather than its basis.

More generally, 'orthographic transparency' – the regularity of grapheme–phoneme conversion rules – can be reflected in the size of the units encoded by occipito-temporal neurons. In 'transparent' writing systems such as Italian or the Japanese Kana script, the letter and bigram levels suffices for grapheme-phoneme conversion. In an 'opaque' script, however, such as English or Kanji, a larger-size visual unit, more anterior along the visual hiearchy, must be used. Compatible with this idea, stronger and more anterior activation is observed in the left occipito-temporal region in English than in Italian readers [24], and, at a slightly more mesial location, during Kanji than during Kana reading in Japanese readers [25,26].

Box 3. Unlearning of symmetry generalization during the acquisition of reading

Most of the properties of macaque inferotemporal cortex listed in Box 2, such as size and location invariance, are useful for reading. However, are there properties of the visual system that are actually detrimental to reading acquisition? Mirror-image generalization might be such a property. A principle of mirror generalization seems to have been deeply entrenched by evolution into our visual system, presumably because the identity of most objects in the natural world remains the same under a mirror-image transformation. After exposure to a single image in a fixed orientation, humans and many animals spontaneously treat the mirror-symmetrical version as identical to the original [34,49]. Furthermore, inferotemporal neurons frequently respond identically to mirror-image pairs of objects [50], even if they have been trained with only one view [34] (see Figure I).

Mirror symmetry was present in some ancient writing systems such as Egyptian hieroglyphs and ancient Greek, which could be read in both directions. Strikingly, early on in reading acquisition, many children undergo a 'mirror stage' during which they spontaneously read and write indifferently in both directions [51,52]. As a consequence, they experience confusions between mirror-image letters, which can persist up to adolescence in children with dyslexia [52,53].

We propose that mirror generalization is an intrinsic property of the primate visual system, which must be unlearned when learning to read. The finding that several young children, without training, exhibit a competence for mirror reading and writing, is illuminating for theories of reading acquisition. It is incompatible with a constructivist or 'blank slate' view, according to which exposure to print would create, in a purely bottom-up fashion, neurons tuned to letters and words. It fits, however, with a selectionist hypothesis according to which learning to read proceeds by minimal reconfiguration of a pre-existing architecture evolved for object recognition, and which initially incorporates a principle of mirror-image generalization.
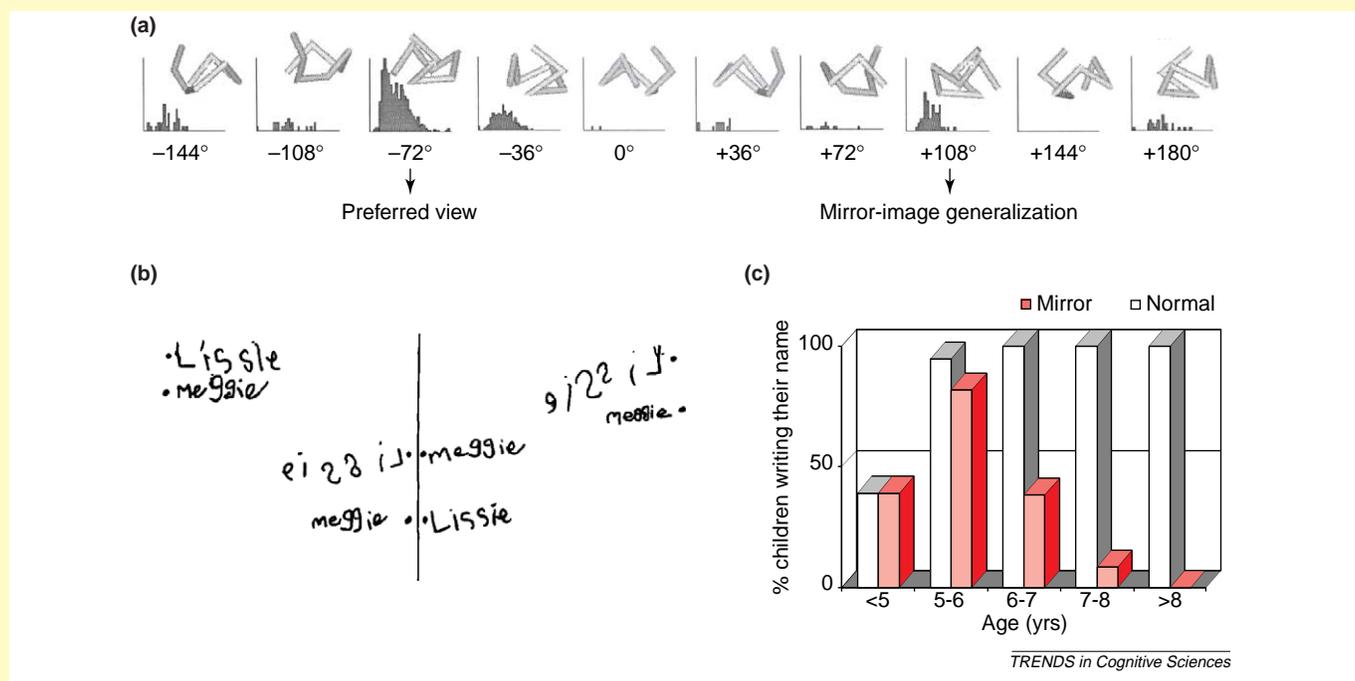

Figure I. (a) Logothetis and Pauls [34] trained monkeys to recognize a wire-frame object from a specific point of view. After training, inferotemporal neurons spontaneously generalized their responses over a 180° rotation around the vertical axis, which corresponds approximately to a mirror-image view. (Reproduced with permission from [34].) (b) Two children were asked to write their name next to the black dots. When she lacked space, Lissie, who was five, spontaneously wrote in mirror image. Meggie, who was six, always wrote normally. (Reproduced with permission from [55], after [51].) (c) The percentage of children of different ages who could write their first name in normal or mirror-image writing. Many children, around the age of 5–6 yrs, go through a brief period in which they can write indifferently in both directions. (Redrawn from data in [55].)

Predictions and empirical tests

The proposed LCD coding scheme makes explicit predictions which could be tested with neuroimaging and intracranial recording techniques. Although receptive field characteristics cannot be directly assessed by non-invasive methods, they can be tentatively measured indirectly through fMRI adaptation [27], also called 'the priming method' [28]. This technique examines whether the fMRI signal diminishes upon repetition of the same object, possibly with changes in size, location, or shape. The object transformations which yield fMRI adaptation are thought to characterize the average receptive field and invariance structure of neurons in each voxel.

Using fMRI priming, an extended strip of left occipito-temporal cortex, lateral to the fusiform gyrus, has been shown to adapt when a word is repeated, even in a different case (e.g. *RANGE–range*) [29,30]. This fits with the model's suggestion that case invariance can be achieved early on. Furthermore, fMRI has revealed a hierachical organization of this region [31]. In the posterior occipitotemporal cortex ($y = -68$), priming depends on the presence of single letters at a specific location, and breaks down if the repeated word is offset by one letter. Thus, this area might thus contain the postulated bank of location-specific letter detectors. More anteriorly ($y = -56$), priming resists a small change in letter position, but does not differentiate words and their anagrams (e.g. *RANGE–anger*). This area might therefore be dominated by local bigram detectors. Finally, still more anteriorly ($y = -48$), priming begins to be stronger for

words than for anagrams. At this level, therefore, small strings or even entire words might begin to be coded.

Behaviorally, the LCD model impacts on how one should measure the similarity between words, and in particular how to define lexical 'neighbors'. Currently, lexical neighbors are defined as words of the same length that differ by one letter. We predict that a composite measure, taking into account the proportion of shared letters and bigrams as well as their retinal distances, should provide a better predictor of priming and of lexical confusions. Measuring the influence of letter distance on priming [32], migration [3] and letter transposition effects [7,12,33] may provide a quantitative test of the proposed receptive structure for letter and bigram detectors.

The model also predicts conditions under which fast word recognition should be severely disrupted. Letter detectors should be disrupted by rotation ($>40°$ according to monkey electrophysiological data [34]). Bigram detectors should be disrupted by spacing of the component letters (e.g. H O U S E), with a sudden reading difficulty once the blank space exceeds approximately two letter widths.

Finally, if word recognition builds upon a pre-emption of object recognition skills, one might expect mirror invariance to be present when children first learn to read, and to be later unlearned in the course of becoming an expert reader (see Box 3).

Conclusion

From a neurophysiological perspective, the internal code for visual words is unlikely to be of the rational and minimal type postulated in cognitive psychology. Rather, we expect a diverse, redundant repertoire of reading-related neurons, resulting from small modifications of the pre-existing primate visual system. This model thus opens up the exciting possibility of using the considerable

neurophysiological information available on the primate visual cortex to inform models of reading and its acquisition (see also Box 4).

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