

**Anatomy and physiology of word-selective visual cortex: From visual features to lexical processing**

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## **Abstract**

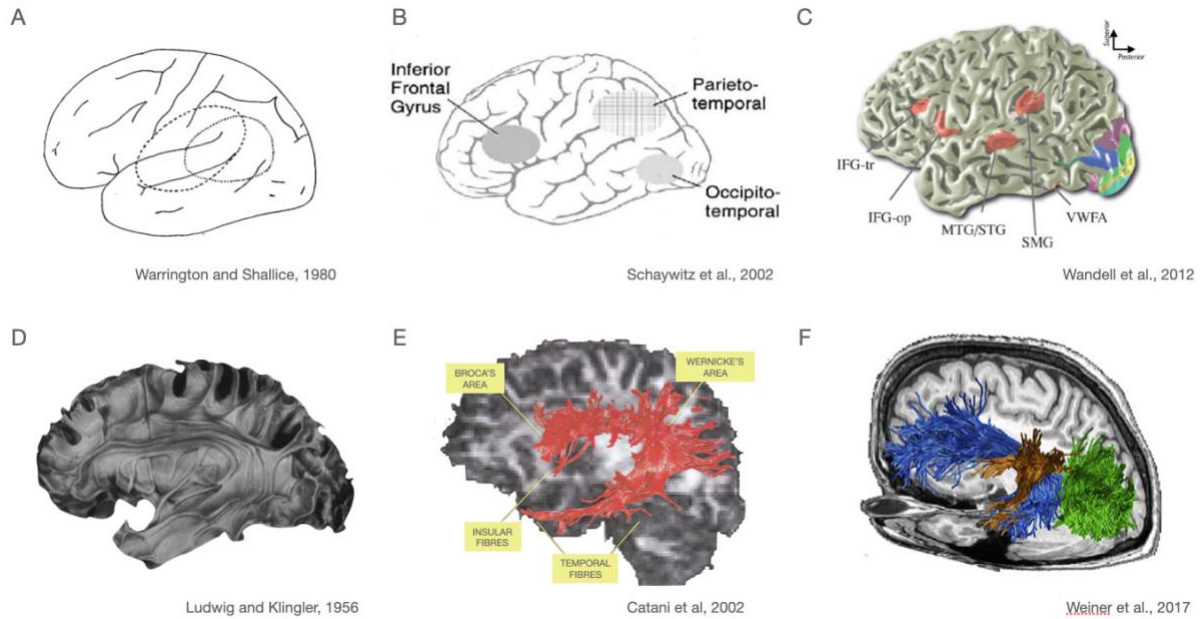
Over the past two decades, researchers have tried to uncover how the human brain can extract linguistic information from a sequence of visual symbols. The description of how the brain's visual system processes words and enables reading has improved with the progressive refinement of experimental methodologies and neuroimaging techniques. This review provides a brief overview of this research journey. We start by describing classical models of object recognition in non-human primates, which represent the foundation for most of the early models of visual word recognition in humans. We then review functional neuroimaging studies investigating the word-selective regions in visual cortex. This research led to a differentiation of highly specialized areas, which are involved in the analysis of different aspects of written language. We then consider the corresponding anatomical measurements and provide a description of the main white matter pathways carrying neural signals crucial to word recognition. Finally, in an attempt to integrate structural, functional, and electrophysiological findings, we propose a view of visual word recognition, accounting for spatial and temporal facets of word-selective neural processes. This multi-modal perspective on the neural circuitry of literacy highlights the relevance of a posterior-anterior differentiation in ventral occipitotemporal cortex for processing visual and lexical features. It also highlights unanswered questions that can guide us towards future research directions. Bridging measures of brain structure and function will help us reach a more precise understanding of the transformation from vision to language.

Keywords: reading; ventral occipitotemporal cortex; word recognition; fMRI; VWFA; diffusion MRI

## Introduction

Literacy presents a fascinating challenge for neuroscientists and cognitive scientists alike: written text reaches the retina as patterns of light and, within a couple hundred milliseconds, these visual signals are transformed into sound and meaning. Beginning in the 1990s, early neuroimaging research detailed the core parts of the brain's reading circuitry revealing: (a) the cortical regions involved in different aspects of reading, (b) the major white-matter tracts that carry signals between these regions and (c) how the development of this circuit is related to the process of learning to read (Figure 1). For example, by the early 2000s it was widely accepted that a region of ventral occipitotemporal cortex (VOTC), termed the visual word form area (VWFA), is involved in rapid and automatic word recognition (Cohen et al. 2002; McCandliss et al. 2003), and that a region in the superior temporal cortex is involved in encoding the sounds of language (Graves et al. 2008; Pugh et al. 1996). Following the overall trend of mapping the brain during this era, and using available imaging techniques, this level of description provided first answers to the question of *where*, as opposed to *how*, reading is implemented in the cortex. Despite progress in detailing the parts list of the reading circuitry, the fundamental challenge of understanding how written text as visual input is transformed into language remained elusive.

A recent surge of papers combining detailed anatomical methods, high-resolution fMRI measurements, and intracranial electrophysiology recordings in the human brain, supports new insights into the mechanisms that underlie the transition from parallel processing of visual features to the extraction of lexical properties from text (White et al. 2019). These new findings both confirm the predictions of classic models and reveal unforeseen properties of the neural architecture underlying word recognition. In this paper, we first provide a retrospective on the research that shaped the way we think about the visual word form circuitry and laid the foundation for the most influential models of word recognition in humans. Second, we review recent functional neuroimaging findings that moved the field from the premise of a single VWFA to a more granular understanding of the sequence of word-selective visual regions that encode various aspects of written language. This transition in the field is supported by spatially distinct neural responses to different properties of written language within the large swath of VOTC that has been termed the VWFA. Third, we summarize the anatomical literature detailing the white matter anatomy of VOTC and its structural connectivity to other regions of the reading circuit. Finally, we bring the functional and structural literatures together by summarizing the flurry of recent publications that detail the computations of word recognition at a new level of precision. These new observations raise questions that foreshadow future efforts to understand how the brain's visual system enables reading.



**Fig. 1** History of the reading circuitry. (a) Neurologists of the early 20th century debated the location of word recognition and this debate played out through the early days of PET until the VOTC was discovered as the location of the “visual word form area”. The location was first confirmed by neurologists (Warrington and Shallice 1980). This debate was at the spatial scale of lobes. (b) Within the first decade of fMRI the three main components of the reading circuitry were defined as left inferior frontal, inferior parietal and occipitotemporal cortex (Pugh et al. 1996; Shaywitz et al. 2002). This early model continues to be influential and outlines the circuitry at the spatial scale of ~4cm (general locations within a lobe). (c) Over the next decade a more nuanced understanding of these regions emerged. Regions were precisely defined relative to sulcal landmarks at the millimeter spatial scale. Language-related regions are in red, while the other colors are used to illustrate retinotopic maps in the visual cortex (Wandell et al. 2012). (d, e, f) A similar historical progression of anatomical precision for white matter pathways. (d) Ludwig and Klingler’s brain model provides a representation of the white matter tracts. Using Klingler’s method of dissecting the human brain after freezing it, these models revealed the structure of axonal connections into large bundles or fascicles. (Ludwig and Klingler 1956). (e) Early diffusion tensor imaging based tractography showing a major white matter pathway connecting regions involved in language processing. These in-vivo white matter tract reconstructions corroborated previous post mortem anatomical findings (Catani et al. 2002). (f) Recent advances in diffusion MRI allow fine-grained representation of white matter pathways in relation to functionally defined regions within individual brains (Yeatman et al. 2012; Weiner et al. 2017; Takemura et al. 2015). The current state-of-the art has led to predictions of functional responses in individual brains, with millimeter precision, based on diffusion MRI measures of an individual’s white matter anatomy (Saygin et al. 2012; Grotheer et al. 2021). In each row there is a gradual increase of precision and spatial resolution, which became possible with the accumulation of knowledge from different modalities and the concomitant improvement in imaging technologies. Our current understanding builds upon these previous models and several aspects of the reading circuit are still being investigated in this rapidly evolving field of research.

## **The ventral visual stream and theories of word recognition**

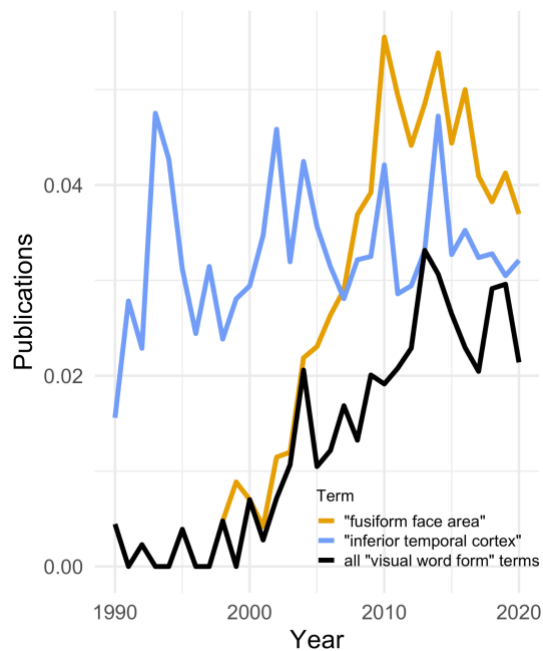
The notion of a visual word form area, or region of visual cortex that develops with literacy to instantiate expertise in the patterns of written language, dates back to neurological case studies in the 1800s (Déjerine 1891; Bub et al. 1993; Graves 1997). Modern theories describing the series of operations performed by the human visual system to process written language are grounded in the neurophysiology of object recognition in the macaque ventral visual stream. In macaque, a series of regions beginning in early visual cortex (i.e., V1 and V2), progressing through intermediate stages (i.e., V4), and continuing to inferior temporal (IT) regions (TE, TEO) compute increasingly abstract representations of visual images supporting object recognition (Gross et al. 1967, 1972; DiCarlo et al. 2012). The macaque ventral visual stream is often modeled as a hierarchy where each region inherits the representation computed by the previous region, pools over a larger portion of visual space, and constructs a new representation with greater invariance to properties such as size and location on the retina that are not important for recognition (Riesenhuber and Poggio 1999; Hung et al. 2005; Khaligh-Razavi and Kriegeskorte 2014). The goal of this architecture is to achieve neurons that are selective for specific objects (or categories of objects) and invariant to the low-level properties of those objects. For example while neurons in V1 selectively respond to edges at a specific retinal location and orientation (Hubel and Wiesel 1962; Hubel 1995; Heeger et al. 1996), neurons in V4 selectively respond to line junctions at specific angles over a larger portion of retinal space (Nandy et al. 2013; Kim et al. 2019). Neurons in IT respond to specific shapes over a much larger portion of the visual field (Rust and Dicarlo 2010; DiCarlo et al. 2012). Thus, by integrating adjacent features at multiple stages, recordings from IT neurons can distinguish different types of objects irrespective of their exact location, orientation or luminance. It is interesting to note that when young macaques are trained to recognize letters they develop a region in IT cortex that selectively responds to letter shapes and might be homologous to the word-selective regions in the human occipitotemporal sulcus (OTS) that instantiate expertise with written language (Srihasam et al. 2012, 2014).

Word recognition was hypothesized to depend on a similar hierarchy in the human brain whereby neurons in early visual cortex detect line segments at specific locations, neurons in intermediate visual stages (e.g., hV4) combine these features to detect individual letters at specific locations, and neurons in VOTC assemble combinations of letters to detect individual words (Dehaene et al. 2005). This late stage of processing images for visual word recognition is believed to occur in the “visual word form area”, a region of VOTC that selectively responds to written language (Dehaene et al. 2002; Hasson et al. 2002; Dehaene and Cohen 2011). First evidence for this hierarchy came from studies finding a spatial gradient of sensitivity to orthographic properties of text (Kronbichler et al. 2004; Binder et al. 2006; Brem et al. 2006; Vinckier et al. 2007).

This work laid the foundation for the idea of a hierarchical system supporting word recognition in the fusiform gyrus that then led to studies probing anterior and posterior parts of this system for print sensitivity, orthography effects, and functional connectivity to other brain regions (van der Mark et al. 2009, 2011).

The idea that visual word form processing involves a series of cortical regions with specific functional properties reflects what we know about the visual system: a set of regions process specific aspects of visual input, such as motion, color, shape and retinal location. Even within specific categories of visual objects such as faces, different features seem to be encoded in separate regions (Freiwald and Tsao 2010). Objects that are behaviorally relevant for a species are likely recognized by combining this information that is encoded in different visual regions. However, the details of the computations performed by specific VOTC regions within this posterior-anterior axis remained hypothetical and many questions remained unanswered: Does activation in the left VOTC flow through a gradient or reflect distinct computations performed by specific subregions? Are VOTC regions organized in a hierarchy? At what point are visual features combined to compute an invariant representation of a word? How does the visual system interface with language regions to transition from visual processing of image features to the extraction of lexical properties from text?

**Fig. 2** Use of the term visual word form area in publications. Number of publications mentioning the terms “visual word form area”, “visual word form areas”, “visual word form system”, “visual word form” AND “brain” from 1990 to 2020 are shown in solid black, demonstrating a rapid increase in the early 2000s. As a comparison, the number of publications including the term “fusiform face area” are shown in yellow, and “inferior temporal cortex” in blue. To account for the overall increase of publications, the number of publications was divided by the total number of publications mentioning the term “visual cortex”. Source: pubmed.gov



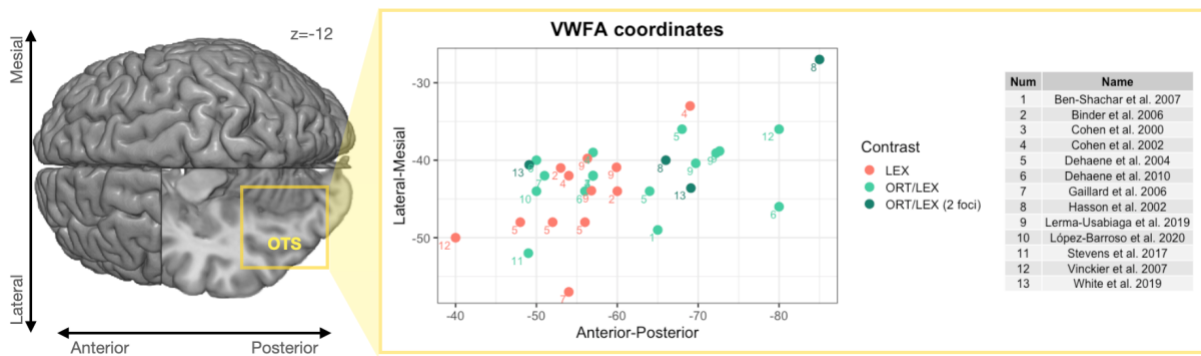
## Functional responses to written words in ventral occipitotemporal cortex

Starting from the early 2000s a major endeavor in neuroimaging research was the spatial localization of functional responses to written language in the human visual system (Figure 2). To this aim, different experimental designs were used to localize the parts of VOTC that preferentially respond to words. fMRI responses to text have been compared to a variety of visual control stimuli (e.g., symbols or false fonts presented in isolation or as a string of characters, as well as other types of non-linguistic visual objects such as faces, tools, houses; (Baker et al. 2007; Cohen et al. 2002; Dehaene et al. 2010; Gaillard et al. 2006; Hasson et al. 2002; Rossion et al. 2003; Stigliani et al. 2015; Ben-Shachar et al. 2007) and a wide range of orthographic stimuli have been examined and compared with each other (e.g., isolated letters, consonant strings, pseudowords, and words; (Glezer et al. 2009; Thesen et al. 2012). These neuroimaging studies consistently reported responses to written language in a portion of left VOTC including the fusiform gyrus and OTS, which can be differentiated from other VOTC areas showing sensitivity to non-linguistic visual object categories such as faces (Malach et al. 2002; Hasson et al. 2002; Grill-Spector and Weiner 2014).

The majority of the abovementioned studies described left VOTC (i.e., the VWFA) as the source of word-selective responses and supported the notion that visual regions specialized for text are located at a high level of the visual system. These word-selective responses have been investigated by probing either perceptual features of words with comparisons of words against non-orthographical stimuli, such as symbols (Hasson et al. 2002; Cohen et al. 2002; Gaillard et al. 2006; Dehaene et al. 2010), or lexical properties, with more fine-grained comparisons of words against letter strings/pseudowords (Cohen et al. 2002; Dehaene et al. 2004; Binder et al. 2006; Gaillard et al. 2006; Vinckier et al. 2007). An examination of the spatial coordinates reported in previous studies shows substantial spatial variability spanning many centimeters of cortex (Figure 3). This variability may be the result of differences in the sampled populations and stimuli, with some studies adopting cross-sectional designs comparing literates and illiterates adults (Dehaene et al. 2010; Skeide et al. 2017), and others comparing children with different levels of reading expertise (Ben-Shachar et al. 2011; Pleisch et al. 2019). In addition, it is also likely that this spatial variability stems from the fact that different stimuli and tasks are, in fact, tapping into different sub-regions within word-selective cortex.

Investigations of the spatial layout of face-, object- and limb-selective regions in humans and macaques have demonstrated a sequence of at least three discrete regions that are selective for each category and span centimeters of the posterior-anterior axis of VOTC (Weiner and Grill-Spector 2010; Freiwald and Tsao 2010; Grill-Spector and Weiner 2014; Weiner et al. 2017a; Park et al. 2017; Bao et al. 2020). Assuming that the cerebral architecture for reading follows organizational principles that are similar to those observed for face and object recognition, we should expect to see multiple word-selective regions that are distributed along the posterior-

anterior axis of lateral left VOTC (White et al. 2019; White et al. 2019; Poeppel et al. 2020). Thus, the variability in the location of word-selective responses across different studies might indicate the presence of a more complex spatial organization of functional responses to written language. In line with this proposal, when previously reported VWFA coordinates are organized based on the type of stimulus contrast, a posterior-anterior differentiation seems to emerge (Figure 3). Specifically, studies that isolated responses to lexical properties of text (e.g., orthographic regularity, frequency) reported activation peaks that cluster in the anterior portion of VOTC ( $y = -40$  to  $-68$ ). On the other hand, studies that employed more general comparisons, where the stimuli differed in both lexical and perceptual properties, the range of reported VWFA coordinates shifts to the posterior portions of VOTC ( $y = -48$  to  $-85$ ).



**Fig. 3** Left: Top view of MNI152 brain template with a cutout over the left occipital temporal sulcus (OTS). Right: Spatial representations of VWFA coordinates reported in a sample of fMRI papers examining different types of stimulus contrasts in adults (Ben-Shachar et al. 2007; Stevens et al. 2017; López-Barroso et al. 2020). Contrasts were categorized as “lexical” when different types of linguistic stimuli were compared (e.g., words vs letter strings, words vs false fonts, words vs pseudowords; as in (Lerma-Usabiaga et al. 2018)). Contrasts were considered “orthographic/lexical” when linguistic stimuli were compared with non-linguistic controls (e.g., letters vs rest, words vs symbol strings, words vs chequerboards; as in (Lerma-Usabiaga et al. 2018)). While the VWFA coordinates of lexical contrasts cluster in more anterior portions of VOTC, the coordinates of orthographic/lexical contrasts cover a wider spatial range and extend further posterior. This spatial variability might be associated with the processing of different features (both lexical and perceptual) that emerge when comparing text with non-linguistic material. Interestingly, two of the abovementioned studies that used an “orthographic/lexical” contrast (marked in dark green) specifically reported two distinct VWFA foci that could be distinguished on the posterior-anterior axis (Hasson et al. 2002; White et al. 2019b). Additional VWFA coordinates can be added to the table available at [INSERT URL UPON PUBLICATION] and the figure can be reproduced and updated using the code available at [INSERT URL UPON PUBLICATION]



This finer-grained differentiation of brain responses to text has been further confirmed by neuroimaging studies that employed multiple experimental contrasts (isolating more perceptual or more lexical features) within the same design (Dehaene et al. 2004; Vinckier et al. 2007; Taylor et al. 2019). For example, (Dehaene et al. 2004) conducted an fMRI priming study where the location and the orthographic similarity between the prime and the target were manipulated. The results showed that, when moving from posterior to anterior coordinates in left VOTC, there was increased sensitivity to orthographic similarity and a concomitant decreased sensitivity to location similarity. Similar results were observed in (Vinckier et al. 2007), where orthographic regularity was gradually manipulated to make the visual inputs progressively more similar to real words (i.e., infrequent letters, frequent letters, frequent bigrams, frequent quadrigrams). Moving towards anterior locations in VOTC was associated with an increased selectivity for word-like stimuli as compared to nonwords. Overall, these findings suggest that while posterior portions of left VOTC represent the perceptual features of written language, anterior portions of left VOTC are sensitive to linguistic aspects of the written input (e.g., frequency, semantic similarity; (Dehaene et al. 2004; Vinckier et al. 2007; Taylor et al. 2019); Figure 3).

It is worth noting that some recent work has made a binary distinction between posterior and anterior word-selective regions in VOTC (i.e., VWFA-1 and VWFA-2 (White et al. 2019b) or pOTS and mOTS (Lerma-Usabiaga et al. 2018), respectively; for earlier evidence see (Hasson et al. 2002; Stigliani et al. 2015)). These two discrete word-selective regions have been differentiated not only based on their function but also based on (a) cytoarchitecture and (b) structural connectivity. Specifically, VWFA-1 responds to visual features that define written language and it analyzes this information in parallel when multiple stimuli are presented simultaneously at different locations in the visual field (Lerma-Usabiaga et al. 2018; White et al. 2019b). In contrast, the VWFA-2 is sensitive to orthographic and lexical properties of the linguistic input and it appears to process information in a sequential fashion, one word at a time (Lerma-Usabiaga et al. 2018; White et al. 2019b). In addition, VWFA-2 responses seem to be more left-lateralized as compared to VWFA-1, likely reflecting the fact that VWFA-2 is involved in analyzing the linguistic aspects of written language (Hasson et al. 2002; Vinckier et al. 2007; Weiner et al. 2017b; White et al. 2019b).

Two additional pieces of evidence further support the functional differentiation between regions of anterior and posterior word-selective cortex. First, intracranial electrophysiological recordings have shown a temporal dissociation between early orthographic effects (~150-250 ms) and late prelexical/lexical responses (~300-500 ms; (Hirshorn et al. 2016; Woolnough et al. 2020), which seems to follow an posterior-anterior spatial topographic distribution (Nobre et al. 1994; McCarthy et al. 1995; Nobre and McCarthy 1995; Lochy et al. 2018; Boring et al. 2020). For example, Thesen and colleagues found that a posterior VOTC region differentiated letters from

false fonts 60ms before a more anterior VOTC region differentiated words from orthographically implausible strings of consonants (Thesen et al. 2012). This is consistent with classic electrophysiological models of visual word recognition, where evoked responses to low-level perceptual features are temporally localized at an early stage as compared to evoked responses to lexical/semantic aspects of the linguistic stimulus (although the spatial localization of these electrophysiological effects is underspecified; (Hauk et al. 2006; Holcomb and Grainger 2006; Barber and Kutas 2007; Grainger and Holcomb 2009). Second, neuroimaging studies examining bottom-up and top-down effects on VOTC have further highlighted the relevance of a posterior-anterior distinction. While bottom-up effects were most likely localized to posterior portions of left VOTC (Kay and Yeatman 2017), top-down effects came from more anterior brain regions and propagated posteriorly (Heilbron et al. 2020; Woolnough et al. 2020).

### **Rethinking the functional organization of ventral occipitotemporal cortex**

The recent functional characterization of different word-selective patches in VOTC has advanced our understanding of visual word recognition. However, it should be noted that there has been a lack of clarity on the extent to which this posterior-anterior organization corresponds to (a) a gradual change or gradient of functional responses versus (b) a sequence of functionally distinct brain regions. In other words, it is still unclear whether the VWFA should be considered a unitary “area” showing a continuous range of sensitivity from perceptual to linguistic properties (Dehaene et al. 2004; Vinckier et al. 2007), or rather a “collection” of multiple discrete subregions specialized for different types of computations on words (White et al. 2019b, a). It is worth noting that these two possibilities are not mutually exclusive. Depending on the level of spatial resolution applied, a sharp categorical distinction might appear as a gradient. Moreover, within a given region there are often cortical columns with discrete specializations. At the millimeter resolution, fMRI studies on visual object recognition have been able to localize functionally distinct VOTC areas that do not overlap (Grill-Spector and Weiner 2014). However, at the resolution of individual neurons, some regions appear to have relatively homogenous populations of cells while others show substantial heterogeneity, (Tsao et al. 2006; Park et al. 2017; Bao et al. 2020). Even within a VOTC region that is highly selective for a visual category (e.g., places) the proportion of neurons showing a category-specific response can vary between 30% and 90% (Tsao et al. 2006; Bell et al. 2011). Hence, while in neuroimaging studies distinguishing between a gradient and discrete areas is still highly informative, when we move to single voxels, there still might be gradients or intermingled populations of neurons within the voxel. Progressive improvements in measurement techniques and theories will help us reconcile these different levels of description. Just as models of word recognition have found improved precision over the last century (Figure 1), we can expect more precise models of the VOTC reading circuitry in the years and decades to come.

As reviewed above, recent evidence supports the idea that the VOTC has (at least) two functionally distinct areas that selectively respond to words (Lerma-Usabiaga et al. 2018; White et al. 2019b, a). At first, this new proposition of two separate VWFAs (or VWFA subregions), with a posterior subregion being responsible for processing perceptual aspects of written text and a more anterior subregion enabling automated lexical processing of words, seems to contradict the literature of the past two decades which was largely driven by the assumption of a single VWFA. However, previous studies have acknowledged a wide spatial distribution of word-selective responses (Cohen et al. 2000, 2002; Hasson et al. 2002), with some suggesting that spatially distinct portions of the VWFA might be attributed to separate functions (Cohen and Dehaene 2004; Dehaene et al. 2004). This proposal is conceptually in line with the studies showing a gradual sensitivity to lexical features on the posterior-anterior axis (Vinckier et al. 2007; Taylor et al. 2019). A closer look at the reported coordinates of the VWFA may suggest that many of the early studies only described one of the two regions, the anterior/middle (classical VWFA; VWFA proper; (Cohen et al. 2000) or the posterior VWFA (Ben-Shachar et al. 2011; Kay and Yeatman 2017; Yeatman et al. 2013; Rauschecker et al. 2012); see Figure 3). In addition, the practice of defining the location of the VWFA based on group analyses in template space or based on previous studies/samples found in the literature may have “smeared” the signal coming from distinct areas and made it appear as one large word-selective patch in VOTC with a gradually increasing sensitivity to lexical features. As our understanding of the VOTC anatomy improves, and the structural pathways that connect to it are described in more detail, we will be able to develop a more complete model that not only describes visually evoked differences in functional responses but also accounts for anatomical boundaries within VOTC.

Hence, the methodological choices made to localize the VWFA have a great impact on the level of precision with which its spatial organization can be described (Glezer and Riesenhuber 2013; Wandell et al. 2012). Using localizer scans and defining the VWFA within individual brains will help us reach a more detailed understanding of the sequence of computations that underlie word recognition. Additionally, greater emphasis on linking the function and anatomical organization of VOTC (in both humans and non-human primates) will help us better characterize the nature of sub-divisions within word-selective cortex (see next sections).

### **White matter connections of ventral occipitotemporal cortex indicate a posterior-anterior distinction**

In the last two decades advances in neuroimaging methods have opened the possibility to explore white matter anatomy with a high degree of precision (Wandell 2016; Jeurissen et al. 2019), and relate white matter anatomy to functional responses at the level of individual subjects. Modern

diffusion MRI (dMRI) measurements in combination with tractography algorithms make it possible to reliably track structural connections between brain areas (Kruper et al.; Yeatman et al. 2012b, 2014; Pestilli et al. 2014; Takemura et al. 2016; Wandell 2016; Jeurissen et al. 2019), providing the basis for a deeper understanding of the nature of functional brain responses and their possible interactions with other structurally connected neural sources. In the case of the VOTC, a detailed structural description of the human ventral stream has revealed major white matter connections to both attention- and language-related brain areas (Yeatman et al. 2013, 2014; Takemura et al. 2015; Weiner et al. 2017b; Lerma-Usabiaga et al. 2018; Chen et al. 2019). The posterior-anterior organization observed in the functional domain (see previous section) is also evident in terms of anatomical connectivity: posterior versus anterior word-selective regions have distinct structural connections. Specifically, recent tractography studies have revealed that posterior portions of VOTC primarily connect to parietal regions involved in the allocation of attention through vertical tracts, namely the left vertical occipital fasciculus (Yeatman et al. 2014; Takemura et al. 2015). On the other hand, mid/anterior portions of the VOTC primarily connect to frontotemporal regions that are essential for language analysis (e.g, Broca's area) through the left arcuate fasciculus (Yeatman et al. 2014; Weiner et al. 2017b; Lerma-Usabiaga et al. 2018)

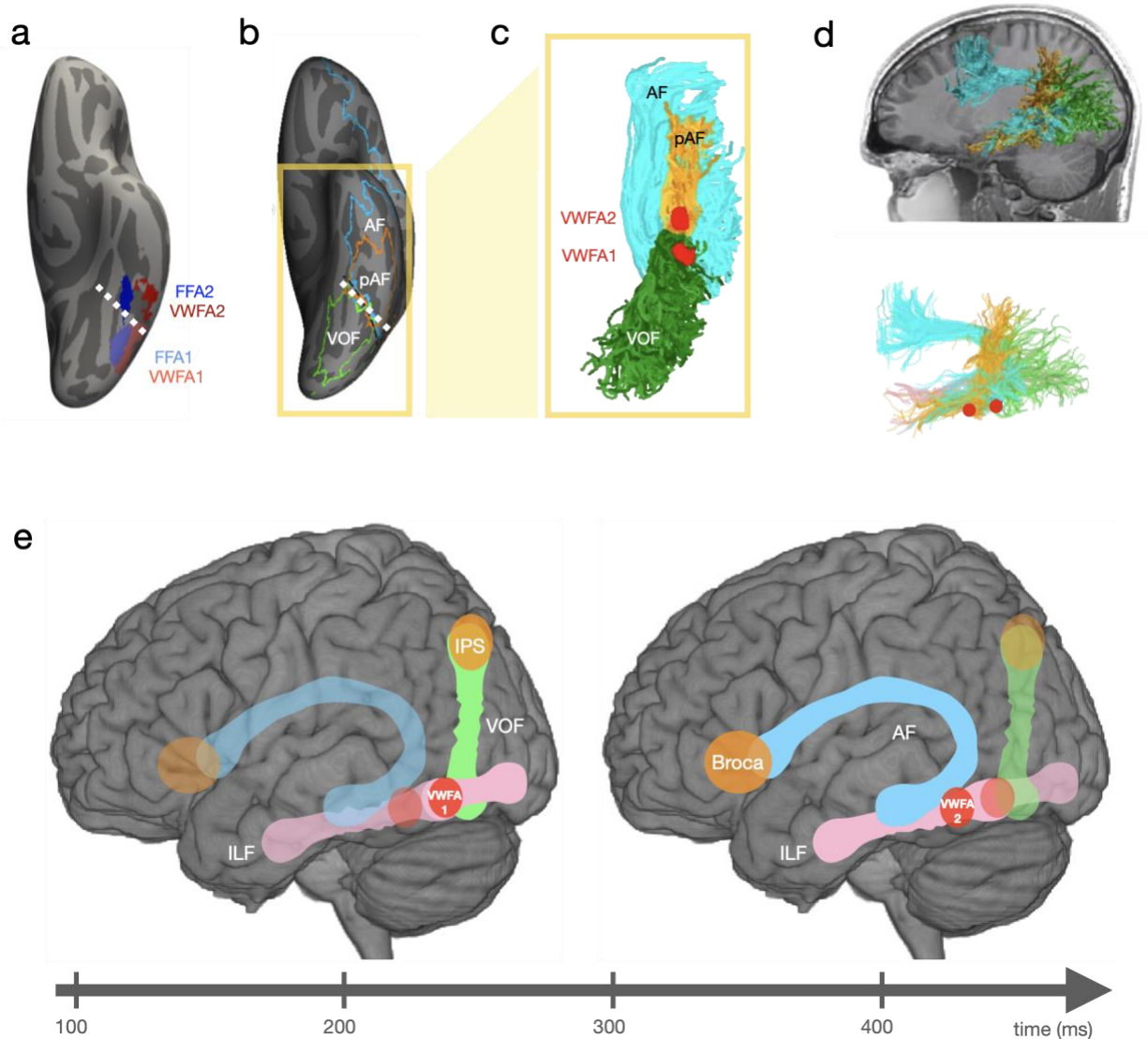
This structural distinction is also aligned with new insights coming from studies focused on the cellular architecture of the cortex. Recent cytoarchitectonic evidence has revealed a sequence of regions in VOTC with distinct cellular structure. Specifically, four cytoarchitectonic areas have been identified in the fusiform gyrus and nearby sulci (FG1, FG2, FG3, and FG4, respectively; (Caspers et al. 2013; Lorenz et al. 2017). Critically, VWFA-1 and VWFA-2 seem to be localized in brain areas that have qualitatively different cellular architectures: While functionally-defined VWFA-1 lies within cytoarchitectonically-defined FG2, VWFA-2 is within FG4 (Weiner et al. 2017a). Other similar relationships between functionally-defined regions and cytoarchitectonic structures have been observed in human and non-human primates (Zangenehpour and Chaudhuri 2005; Borra et al. 2010; Weiner et al. 2017a).

### **Bridging functional and structural evidence of the posterior to anterior VOTC organization**

The distinction between posterior and anterior in VOTC has been observed based on multiple types of measurements. Posterior-anterior differences have emerged in: (1) the functional sensitivity of VOTC responses to written language, (2) the time course of VOTC responses, (3) the structural connectivity between VOTC and other brain regions, and (4) the cytoarchitecture of VOTC. In this section we try to bridge the results from these distinct domains and highlight important future research directions.

Based on the findings reviewed above, we propose how information is processed in a sequence of regions within the visual word recognition system (Figure 4). When a written stimulus is presented, posterior portions of VOTC show an early sensitivity to perceptual properties of the orthographic input, and this early visual response can be flexibly modulated based on structural connections with attentional networks (e.g., vertical occipital fasciculus connecting posterior VOTC to the intraparietal sulcus; (Yeatman et al. 2014; Takemura et al. 2015; Weiner et al. 2017a; Lerma-Usabiaga et al. 2018; Chen et al. 2019). At this early temporal stage (~150-250 ms after stimulus onset), the processing of low-level visual features that compose written language is carried out in a parallel fashion (White et al. 2019b). On the other hand, anterior portions of the VOTC show a later sensitivity to higher-order linguistic properties of the visual input (~300-500 ms after stimulus onset), which can be prioritized and further processed through connections with language areas (e.g., arcuate fasciculus connecting anterior VOTC with Broca's area; (Yeatman et al. 2014; Weiner et al. 2017a; Lerma-Usabiaga et al. 2018; Chen et al. 2019). At this stage, the visual word form processing seems to proceed in a serial fashion: one word at a time (White et al. 2019b). Hence, this posterior-anterior distinction supports the presence of a functional and structural transition from vision to language. Although this proposal needs further confirmations and clarifications, it highlights new research directions and formulates more specific research questions about the reading circuitry.

Additional studies showing a double dissociation between anterior and posterior VOTC functional responses would further confirm the transformation from vision to language. In line with what the literature suggests so far, anterior portions of VOTC (i.e., VWFA-2) should be sensitive to linguistic features (e.g., frequency) but not to low-level perceptual properties (e.g., location) of written words, while posterior portions of VOTC (i.e., VWFA-1) should show the reversed response pattern. Similarly, the allocation of spatial attention should only affect responses in posterior portions of VOTC, and not anterior areas. In addition, many questions related to the emergence of the posterior-anterior VOTC differentiation remain unanswered. Given the structural and cytoarchitectonic differences observed in VOTC, we can expect that during reading acquisition anterior and posterior portions of VOTC might show different developmental trajectories. However, longitudinal studies at this level of precision are sorely lacking. For example, examining prereaders' white-matter pathways that are important for future reading skills might help us predict the location of word-selective VOTC areas. We expect that while the endpoints of the left vertical occipital fasciculus guide the future location of VWFA-1, the endpoints of the left arcuate fasciculus guide the emergence of VWFA-2. Similarly, functional connectivity patterns observed in the developing brain might help predict the functional specialization of VWFA subareas (O'Rawe et al. 2019; Li et al. 2020).



**Fig. 4 Upper panel:** A. Surface localization of VWFA-1, VWFA-2, FFA-1 and FFA-2. Unpublished data from a sample of adult typical readers performing a category recognition experiment. Colored patches denote the location of maximal overlap of individually identified regions transformed to the fsaverage cortical surface with surface-based alignment (Fischl 2012). B. Cortical endpoints of the left arcuate fasciculus (AF), the posterior arcuate fasciculus (pAF) and the vertical occipital fasciculus (VOF, from (Weiner et al. 2017b)). C and D. Ventral and sagittal view of VWFA-1, VWFA-2, AF, pAF, and VOF. Data are from an example adult participant. In D, the upper plot shows AF, pAF and VOF superimposed on the participant's T1 weighted image. The lower plot in panel D shows the AF, pAF, VOF, the inferior longitudinal fasciculus (ILF), VWFA-1 and VWFA-2. **Lower panel:** Schematic representation of VWFA subdivisions and anatomical connections subserving early (150-250ms) and late (300-500ms) word-recognition processes.

## **Conclusion**

The progressive refinement of our models of the brain's reading circuitry have resulted in a better understanding of how the brain can extract linguistic information from a visual input (Figure 1). In some ways, our understanding of the brain's reading circuitry has remained relatively consistent across the decades. For example, it was over a century ago when (Déjerine 1891) originally proposed the notion of a visual word form area and early fMRI work documented many fundamental properties of this swath of VOTC. However, in other ways, the level of precision in current models of the brain's reading circuitry would have been unimaginable in the early days of fMRI. For example, a sequence of specific regions that perform distinct operations can now be reliably localized in an individual's brain, and relative to the white matter connections that communicate information throughout the reading circuitry. Continued progress, and incremental refinement of our models, will depend on integrating structural and functional measurements at finer spatial and temporal scales, and building theories that bridge vision science, linguistics and cognitive neuroscience.

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### **Conflicts of interest/Competing interests**

The authors have no relevant financial or non-financial interests to disclose.

### **Availability of data and material**

Data to reproduce the reported figures are available at [INSERT URL UPON PUBLICATION]

### **Code availability**

Code to reproduce the reported figures is available at [INSERT URL UPON PUBLICATION]

### **Authors' contributions**

All authors drafted and/or critically revised the work, SC and IK performed the literature and data search for figure preparation.



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