Check for updates

Beyond the Visual Word Form Area – a cognitive characterization of the left ventral occipitotemporal cortex

Agnieszka Dębska[1]*, Marta Wójcik[1], Katarzyna Chyl[1,2], Gabriela Dzięgiel-Fivet[1] and Katarzyna Jednoróg[1]

[1]Laboratory of Language Neurobiology, Nencki Institute of Experimental Biology, Polish Academy of Sciences, Warsaw, Poland, [2]The Educational Research Institute, Warsaw, Poland

The left ventral occipitotemporal cortex has been traditionally viewed as a pathway for visual object recognition including written letters and words. Its crucial role in reading was strengthened by the studies on the functionally localized "Visual Word Form Area" responsible for processing word-like information. However, in the past 20 years, empirical studies have challenged the assumptions of this brain region as processing exclusively visual or even orthographic stimuli. In this review, we aimed to present the development of understanding of the left ventral occipitotemporal cortex from the visually based letter area to the modality-independent symbolic language related region. We discuss theoretical and empirical research that includes orthographic, phonological, and semantic properties of language. Existing results showed that involvement of the left ventral occipitotemporal cortex is not limited to unimodal activity but also includes multimodal processes. The idea of the integrative nature of this region is supported by the broad functional and structural connectivity with language-related and attentional brain networks. We conclude that although the function of the area is not yet fully understood in human cognition, its role goes beyond visual word form processing. The left ventral occipitotemporal cortex seems to be crucial for combining higher-level language information with abstract forms that convey meaning independently of modality.

1. Introduction

The unprecedented interest of neuroscientists in the structure and function of the left ventral occipitotemporal cortex (VOT) came from the fact that this region has over the years been systematically reported as particularly responsive during processing of written words (McCandliss et al., 2003; Dehaene and Cohen, 2011). Typically language-related left VOT is anatomically situated within the left occipitotemporal sulcus extending to the left fusiform gyrus and inferior temporal gyrus (Price and Devlin, 2011; Price, 2012; Lerma-Usabiaga et al., 2018).

The term Visual Word Form Area (VWFA) – functionally localized in most studies in the mid-anterior part of the left VOT – was mostly popularized by Cohen et al. (2000, 2002). The most canonical proposition of the VWFA localization given by Cohen et al. (2002) was: $x = -42$, $y = -57$, $z = -15$. Later the meta-analysis by Jobard et al. (2003) of language-based contrasts (e.g., word-fixation and word-consonants) defined the localization at: $x = -44$, $y = -58$, $z = -15$ (see: **Figure 1**). However, the exact localization of the peak is assumed to slightly differ in each individual and was typically tested by comparing activation of the left mid-fusiform for real words versus pseudowords, consonant strings, checkerboards, false fonts, symbol strings, or other letter-like visual stimuli. There is an ongoing debate if the VWFA as a part of higher-level visual cortex should show preferential activation to visual words over other categories of namable visual stimuli such as objects, tools, or faces (see e.g., Price and Devlin, 2003; Szwed et al., 2011; Price, 2012; Nestor et al., 2013; Neudorf et al., 2022). Hirshorn et al. (2016) investigated the visual word form hypothesis using direct brain stimulation and EEG. They focused on the left midfusiform gyrus (lmFG) and discovered that disrupting activity in this region impaired perception of words and letters. The lmFG is involved in different stages of orthographic representation, including low-level visual representation.

In the critical article Price and Devlin (2003) showed that the VWFA ($x = -42$, $y = -57$, $z = -15$) is involved not only in visual word processing but also in naming colors and objects, reading Braille and processing auditory words. This was one of the first pieces of evidence that the middle left VOT area called VWFA is involved in more than only processing visual word forms. What is interesting is that all those tasks were connected to language functions, such as naming (semantics), speech sound processing (phonology), and Braille reading (orthography but in a modality different than visual). Therefore, in the current article, we focus on the language-specific activity of the left-lateralized VOT (LS-VOT) in multiple language-related tasks. We discuss phonological, semantic, and orthographic processing within the LS-VOT independently from visual, auditory, or tactile modality. We start by describing the earliest but also the narrowest understanding of the LS-VOT as a visual-based reading region and extend this by adding different layers of evidence for other possible language-related functions of this area.

2. LS-VOT as a part of the visual letter-related system

The cognitive concept of the Visual Word Form came originally from the Warrington and Shallice (1980) clinical study where authors contrasted two different forms of reading: letter-by-letter and whole words. The ability to extract an abstract orthographic representation of a whole word, irrespective of its color, shape, font, and size constitutes the knowledge of the "visual word form." According to Rapp and Fischer-Baum (2014), orthographic representations may vary in the size of units (morphemes, digraphs, and letters) and should contain information about letter identity, consonant-vowel status, syllabic role, and letter position.

From the beginning, the chosen terminology defined the scope of the investigation as modality-dependent since a VISUAL Word

Form concept drove authors to explore the VWFA as a part of the human visual system. The first studies on the VWFA focused on how reading acquisition transforms the "inferotemporal pathway for visual object recognition" (McCandliss et al., 2003). The visual modality-based approach proposed that LS-VOT is tuned to processing letters based on the constraints in the hierarchical receptive field structure (Dehaene et al., 2005) with a preference for line junctions (Szwed et al., 2011). Accordingly, internal segmentation of the LS-VOT is functionality dependent on the level of word-related form processing. A posterior-to-anterior gradient in selectivity was revealed, where false fonts, letters, bigrams, trigrams, and whole words are processed with increased selectivity in a posterior-to-anterior direction (Vinckier et al., 2007). This gradient is consistent with Dehaene et al.'s (2005) proposal that the left posterior VOT processes single letters, the middle processes bigrams and trigrams, and the anterior processes lexical units. Studies that combine relatively high spatial and temporal resolutions confirm that when showed that letter-selective responses occurred approximately 60 ms earlier than word-selective responses, with phase-locking in anterior areas involved in lexico-semantic processing (Thesen et al., 2012). In this visual-based approach, LS-VOT is treated more as an identifier for visual properties of letters and word-forms based on line junctions than as a part of the language-specific system. However, this perspective poses some problems.

First, it neglects that LS-VOT is structurally (Saygin et al., 2016; Vanderauwera et al., 2018; Moulton et al., 2019) and functionally (Morken et al., 2017; Smith et al., 2018; Li et al., 2020) connected with the language system and especially the left superior temporal gyrus (STG) and inferior frontal gyrus (IFG) which take part in phonological and semantic processing (Hodgson et al., 2021). It seems that not only does shape, size or font determine orthographic form but also its phonology (Pylkkänen and Okano, 2010). In terms of LS-VOT engagement, Hashimoto and Sakai (2004) showed preferential activation to newly learned orthographic forms in adults but only when they were combined with speech sounds instead of non-speech sounds (tones and noise).

Second, orthographic representations are usually understood as modality-independent (Rapp and Fischer-Baum, 2014). In line, the LS-VOT was found to be responsive to reading not only in the visual but also in the tactile modality (Büchel et al., 1998a,b). This was true for both early and congenitally blind individuals (Amedi et al., 2003), some late blind individuals (Burton et al., 2002), as well as sighted individuals learning to read Braille tactually (Siuda-Krzywicka et al., 2016). The site of the reading-related activation was not discernable between the blind and the sighted readers (Reich et al., 2011; Dzięgiel-Fivet et al., 2021) and in both groups, similar sensitivity to letters was found (Rączy et al., 2019). These observations led to a hypothesis that LS-VOT is implicated in reading on a modality-independent level (Amedi et al., 2017).

Third, LS-VOT activation may not be specific to letter shapes as compared to other visual meaningful stimuli like nameable pictures. Neudorf et al. (2022) showed that the same LS-VOT area was equally responsive to naming pictures and words without dominant activations for one type of stimuli. There is also an interesting line of research that broadens the LS-VOT function to all symbolic stimuli with known referents, even those without an orthographic structure or preferred visual properties like line junctions. In a study by Song et al. (2012) the LS-VOT was more
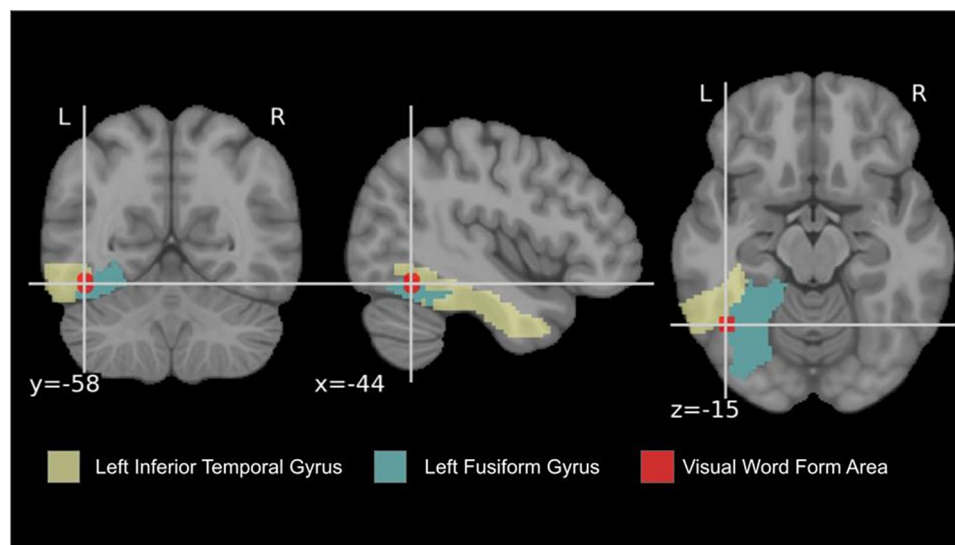
FIGURE 1
Anatomical visualization of the left inferior temporal gyrus and fusiform gyrus; the localization of the word-specific peak from the meta-analysis of Jobard et al. (2003).

active for symbolic landscapes (e.g., Eiffel Tower as a symbol of Paris) than for non-symbolic landscapes (e.g., unknown high building). This effect was also present for the artificial symbol–referent associations that were trained in the study. Preferential LS-VOT activity was further found for stimuli with communicative intentions like body gestures (Xu et al., 2009), or visually complex everyday scenes (Tylén et al., 2009). A more general view was proposed by Vingerhoets et al. (2013) who showed mutual co-lateralization between tool use and language, regardless of handedness. The authors argue that their results link gestures and speech to explain the beginning of human language.

3. LS-VOT as storage for abstract orthographic representations

The idea that the LS-VOT is storage for abstract orthographic forms was widely explored. There is an ongoing debate about whether LS-VOT processes whole-word (lexical) forms or whether LS-VOT is sensitive primarily to smaller orthographic parts like letters or bigrams (Dehaene et al., 2005; Binder et al., 2006). There was also a more hybrid approach claiming that LS-VOT is involved in both lexical and sublexical coding (e.g., Schurz et al., 2010). The sublexical hypothesis which assumed that the LS-VOT is responsive to bigrams or trigrams rather than whole words was challenged by Glezer et al. (2009). The authors employed a rapid adaptation paradigm to detect more subtle changes in BOLD signal than in the usual contrast testing. With this change in methodology, the authors claimed that LS-VOT proved to be selective to real words and not sublexical units. In their study, the comparison of mean activations for two real words that shared visual similarities but were not identical (like "farm" – "form") revealed no neural adaptation patterns contrary to the presentation of two orthographically identical words (Glezer et al., 2009). Thus, sublexical information shared by those words was

not sufficient enough to evoke selectivity in LS-VOT. Further research revealed that LS-VOT's selectivity was also present in processing familiarized (trained) pseudowords in contrast to the novel ones (Glezer et al., 2015). This approach corresponds with another type of research based on the so-called "familiarity effect." It was first observed in object recognition studies when the repeated presentation of the stimuli led to decreased activation of the VOT (Chao et al., 2002; Van Turennout et al., 2003). Following this idea, Kronbichler et al. (2004) tested the LS-VOT response regarding the stimuli arranged gradually from the most familiar (high-frequency words) to the least (pseudowords). Again, the authors demonstrated that the higher the familiarity, the lower the LS-VOT activation, which was interpreted as a proof for the whole-word functionality instead of letter-based functionality: more effort was needed to decode words that did not have familiar forms. In the follow-up study in 2007, Kronbichler et al. (2007) used a different set of items (words/pseudohomophones/pseudowords) and observed the same effect: lower activations of LS-VOT for words versus pseudohomophones and pseudowords [this was widely replicated by Bruno et al. (2008), Woollams et al. (2011), and Wimmer and Ludersdorfer (2018)]. The latest connectivity studies (Lerma-Usabiaga et al., 2018; White et al., 2019; Yablonski et al., 2023) showed that anterior LS-VOT is connected with higher-language areas as opposed to the posterior part connected with visual regions and sensitive to visual features of words. It may suggest the functional division between posterior and anterior parts, where anterior part showed growing multimodality and holistic lexical processing while a posterior part supports this hub by providing information about visual features of letters.

There is a consensus that especially the location of left-hemispheric LS-VOT is very consistent across tasks and writing systems (Bolger et al., 2005; meta-analysis including studies carried out in European alphabets, Chinese characters, and Japanese Kana and Kanji). In children, the overlap of specific activation for reading English words and Chinese characters (Krafnick et al., 2016), as

well as French words and Chinese characters (Feng et al., 2021) was found in the left LS-VOT in the direct proximity of the English-based ROI (Cohen et al., 2002). Classical LS-VOT ROI was also explored in adults reading frequent Chinese characters (nouns), and activation in this region was confirmed as specific for reading (Liu et al., 2008). No language differences and high specificity of the LS-VOT [also located as in Cohen et al. (2002)] were also found in bilinguals reading Chinese and Korean (Bai et al., 2011). Nonetheless, while the LS-VOT engagement was consistent across many studies regardless of the languages and writing systems, its right hemisphere homolog was consistently found to be more engaged in the readers of logographic compared to alphabetic scripts (e.g., Bolger et al., 2005). The bilateral processing of non-alphabetic scripts has been attributed to their visual complexity and the larger grain size principle inherent in these scripts (Hsiao and Lam, 2013); right hemisphere engagement would be thus more associated with holistic or whole-object processing (Hirshorn and Harris, 2022). In line with that Li et al. (2017) showed that, similarly to alphabetic languages, in readers of logographic scripts the connection between spoken language areas and the LS-VOT strengthens as individuals grow older. However, the strength of this connectivity differs between the orthographies, as learning alphabetic languages is mostly based on phonics instructions.

4. Why is LS-VOT sensitive to speech?

Language Specific - VOT (LS-VOT) was traditionally argued to store visual-based orthographic representations. However, many studies so far showed that the LS-VOT is activated in auditory speech-based tasks. This was found in sighted readers (Dehaene et al., 2015; Planton et al., 2019) but also to a larger extent in blind Braille readers. In the case of the blind population, VOT activation was observed during both low-level tasks like passive listening to words (Kim et al., 2017; Dzięgiel-Fivet et al., 2021), basic phonological tasks (Burton et al., 2003; Arnaud et al., 2013) but also during high-level tasks like sentence comprehension where the activity of this region was related to task difficulty (Kim et al., 2017).

Moreover, in the sighted LS-VOT's activation seems to be related to the overall reading level and reading deficits (Dehaene et al., 2010; Desroches et al., 2010; Dehaene and Cohen, 2011; Dębska et al., 2016, 2019; Wang J. et al., 2018, Wang et al., 2021). This is in analogy to the theories of reading which suggest that the involuntary orthographic influence in processing phonology appears as a function of reading skill (Morais et al., 1979; Ventura et al., 2007; Ziegler and Muneaux, 2007). The plethora of empirical evidence favors the abstract, modality-independent concept of the LS-VOT functionality. So far several hypotheses have been formulated that describes an extended LS-VOT role in speech processing.

4.1. A unimodal orthographic hypothesis

Dehaene et al. (2010) and Dehaene and Cohen (2011) proposed a unimodal orthographic hypothesis. Accordingly, abstract orthographic representations are activated automatically

in a top-down manner during active speech processing. In this view VOT activations are not a result of phonological processing but involuntary orthographic co-processing that facilitates and accompanies phonological processing. In Dehaene et al. (2010) study, LS-VOT was active during auditory lexical decision task (distinguishing between words and pseudowords) but not in passive sentence listening. The activity in the auditory lexical decision task was present only in literates but not in illiterates. Individual differences in the strength of LS-VOT activity on auditory stimuli correlated with the LS-VOT activity for written words but not other visual objects. These empirical findings were interpreted as evidence for the unimodal orthographic hypothesis. Ludersdorfer et al. (2015, 2016) asked whether the need for orthographic processing is crucial for LS-VOT's activation in an auditory speech-based task. Results showed that LS-VOT was more active for orthographic (letter count) relative to semantic (living-non-living) tasks (both were based on speech stimuli). However, even the semantic task elicited weak activation relative to the baseline non-linguistic tones processing in the LS-VOT. Most auditory speech-based tasks where the preferential activity of LS-VOT and its positive relation to reading proficiency was acknowledged were not orthographic tasks *per se*. Most empirical data came from phonological awareness tasks like word rhyming (Booth et al., 2002; Desroches et al., 2010; Yoncheva et al., 2010; Dębska et al., 2016), alliteration (Wang J. et al., 2018; Dębska et al., 2019; Wang et al., 2021), or even pseudoword matching (Dębska et al., 2019). The question arises if the preferential activity of LS-VOT in speech-based tasks requires the active engagement of orthographic code [like Dehaene et al. (2010) directly proposed], or if LS-VOT is crucial for processing phonological or semantic properties of language independent of the need to activate orthographic code (see sections "2. LS-VOT as a part of the visual letter-related system" and "4.2. A unimodal phonological hypothesis").

Another issue is that the LS-VOT might play a different role in the speech-based task than in processing written stimuli. For example, Ludersdorfer et al. (2013) showed that in the case of visual stimuli, the LS-VOT reduced its activity for word-like written stimuli (words < pseudowords < artificial stimuli) but in reverse increased its activity for word-like auditory stimuli (words and pseudowords > artificial stimuli). Also, observed LS-VOT engagement during the processing of speech might be related to the deactivation effects more than activation differences. For example, Yoncheva et al. (2010) controlled the attentional demands of two tasks: one speech-based and one non-linguistic (tones comparison). The comparison between attentional tone and speech processing showed that both conditions evoked deactivations in the left fusiform except for the more narrow left mid-fusiform area in the case of a speech condition. This leads to higher activity in the mid-fusiform (corresponding to VWFA) relative to surrounding deactivated regions of the left fusiform.

4.2. A unimodal phonological hypothesis

A second explanation of the LS-VOT's preferential activation to speech is the existence of neuronal populations involved in processing phonology. Pattamadilok et al. (2019) formulated a theoretical proposal for the existence of unimodal (auditory) phonological groups of neurons in LS-VOT that are sensitive

to phonological but not orthographic features of stimuli. The preliminary confirming evidence came from the Conant et al. (2020) studies on school-aged children and adolescents. They found that activity in the LS-VOT was modulated by phonological factors such as syllable structure, suggesting that this region is involved in processing the sound structure of language. The authors found that the activity of LS-VOT in discriminating speech-syllables versus non-phonemic stimuli was not only positively related to the reading level but also to categorical phoneme perception skills. The authors concluded that LS-VOT plays a role in both reading proficiency and phoneme perception refinement. Although the authors did not exclude an automatic orthographic co-activation explanation, they rather argued that LS-VOT is responsible for the refinement of speech perception and audiovisual integration (see section "4.3. A multimodality hypothesis").

Moreover, Xue et al. (2006) trained adult individuals with a new visual font for 2 weeks (visual training) and then new sounds for another 2 weeks (phonological training). Interestingly, phonological training evoked more activity in bilateral LS-VOT compared to visual training which made the authors conclude that (bilateral) LS-VOT is engaged in processing phonology or in phonology-orthography integration. Still, the interpretation of results was limited by the fact that the order of training was not counterbalanced.

Another piece of evidence for the phonological function of LS-VOT was brought by Pattamadilok et al. (2009) in a TMS facilitation study. The authors tested whether in orthographic or phonological priming on LS-VOT, a TMS stimulation would facilitate word processing. Results showed only unimodal (orthographic or phonological) but not multimodal facilitation effects. The authors interpreted those findings as a confirmation on the existence of separate phonological and orthographic groups of neurons within the LS-VOT but not multimodal ones. However, the site of the LS-VOT stimulation was chosen based on non-specific individual localizer (words > fixation) therefore the localization of phonological versus orthographic LS-VOT areas is still a matter of debate and probably requires higher spatial resolutions than the ones offered by standard fMRI or TMS (Grill-Spector and Malach, 2001; Price and Devlin, 2003).

4.3. A multimodality hypothesis

One may ask if the positive relationship between orthography-phonology integration in the LS-VOT and the reading level (e.g., Wang J. et al., 2018), may be due to the fact that LS-VOT integrates information from orthography and phonology. Print-speech convergence and audiovisual integration effects in LS-VOT that were found to be reading-related are worth discussing in this context.

First, in the case of print-speech convergence, there is an assumption that literacy acquisition changes the brain in a way that print stimuli start to be processed in the network responsible for spoken language processing (Liberman, 1992; Rueckl et al., 2015; Preston et al., 2016; Chyl et al., 2018). Most of the studies showed print-speech coactivations in relation to the reading level mostly in the left IFG and STG (Frost et al., 2009; Rueckl et al., 2015; Preston et al., 2016; Chyl et al., 2018; Marks et al., 2019):

regions typically involved in speech sound processing. Interestingly the LS-VOT area also showed print-speech convergence in the opaque orthographies like English or Hebrew compared to the more transparent orthographies like Spanish (Rueckl et al., 2015). This effect was evident in English adults (Rueckl et al., 2015) and beginning 7 years old readers (Chyl et al., 2021). However in Chyl et al. (2021) no evidence was found on the relation between print-speech co-activation in LS-VOT and the reading level in English or Polish (see Chyl et al., 2021, Supplementary Material 4). Also, the representational similarity analysis (RSA) in processing print and speech in beginning readers showed no significant overlap in LS-VOT contrary to the left IFG and STG. Different results were found in the case of young Chinese adults (18–26 years olds) where RSA analysis showed that LS-VOT patterns of activation are best explained by orthographic and phonological similarity compared to unimodal processing (Zhao et al., 2017; Qu et al., 2022). So it seems that similar patterns between phonology and orthography might be related to reading ability, yet more cross-linguistic and developmental studies are needed.

Second, in the case of language-specific audiovisual integration, involvement in LS-VOT was found during audio-visual exposure to letters and ambiguous speech sounds (Romanovska et al., 2021). McNorgan and Booth (2015) tested audiovisual integration specifically in LS-VOT in English 8–13 years old children in relation to reading and found that multisensory integration in LS-VOT was modulated by the reading level.

4.4. An "all in one" hypothesis

The last possibility is that orthographic, phonological, semantic, and multimodal groups of neurons coexist within the LS-VOT. Those groups could be spatially separated and therefore it should be possible to identify their individual topography. Alternatively, the areas might not be spatially distinct for different functions and thus the activation patterns measured by multivoxel pattern analysis of the same or similar area will differ depending on the task. These two alternatives are interesting because at the first sight the "all in one" approach allows the reconciliation of different empirical findings. An interesting example of the "all in one" approach is an "impostor" hypothesis proposed by Cohen et al. (2004). When the authors tested written and auditory word processing in VOT they found a multimodal area called LIMA ("lateral inferotemporal multimodal area"). LIMA was localized anteriorly to the canonical localization of VWFA (LIMA = $x = -54$, $y = -52$, $z = -10$, VWFA = $x = -39$, $y = -60$, $z = -18$, Talairach coordinates). During the presentation of written and auditory words LIMA was activated independently of modality whereas the region described as VWFA was active only in response to the visual words. The authors concluded that VWFA and LIMA might be "easily confounded" when interpreting the results of fMRI studies (see also Sebastian et al., 2014). Curiously, the authors gave LIMA a function that was later discussed in the context of VWFA: an integrative hub of cross-modal phonemic and lexical links (Price and Devlin, 2011). The "all-in-one" approach is promising because instead of focusing on VWFA defined as an area preferentially activated to real words, the focus is placed more on processing different functions like orthography or phonology or both those

types of information within the VOT. The question is how those spatially different groups of neurons or functionally different patterns of activations should be localized on the individual level, analogically to how VWFA was localized. The promising approaches of using fMRI rapid adaptation (Weiner et al., 2010) or fast periodic stimulation (Gao et al., 2018) are yet to be developed. Interesting insights came from multivoxel pattern analysis research (MVPA). A univariate analysis, which averages brain activation across voxels, could fail to detect weak but informative signals distributed in multivariate patterns (Tong and Pratte, 2012). Different neural patterns are suggested to be associated with different cognitive functions, therefore, may distinguish between various roles of LS-VOT. Also, the MVPA might be more sensitive to individual differences in word processing and reading styles (Carlos et al., 2019). Fischer-Baum et al. (2017) showed that the same region of LS-VOT encodes orthographic and semantic (but not phonological) information. This semantic processing seems to be task- and category-dependent and may contribute to orthographic identification and overall task performance (Wang X. et al., 2018). Another promising approach was presented by Kay and Yeatman (2017). Their model for faces and words demonstrates that high-level representations in the cortex are built from and tied to low-level properties through linear and non-linear operations. This suggests that visual features hierarchically contribute to semantic representations. The model provides a potential mechanism for the emergence of semantic tuning properties in the visual cortex.

5. LS-VOT as a part of distributed neural systems

The research described so far was mostly based on the assumption of a localist representation system, which means that it assumes one set of neurons that is responsible for processing one concept. Instead, a distributive approach may be taken into account (e.g., Roy, 2017) where the whole collective brain network is responsible for encoding a concept. This is an interesting approach because it seems to reconcile different lines of research. For example, there is tension between the purely unimodal nature of LS-VOT and its multimodal characteristics. In the case of distributed system approach, we may treat the LS-VOT as a part of the multimodal network but the function within that network may be unimodal or may vary across tasks (e.g., see Price and Devlin, 2011). Also, the discussion on the LS-VOT's sensitivity for active speech tasks rather than for passive listening, may be informed by the research on connections between LS-VOT and the attention network. If LS-VOT is a part of two cortical networks, the differences in the activity of LS-VOT in active speech tasks vs. passive listening may be a result of the interaction between roles the left VOT plays in language and attention networks. If this is the case, firstly, we may ask what is the empirical evidence on the existence of structural and functional connections between LS-VOT and other brain parts. Secondly, we might wonder what kind of theory would describe the role of LS-VOT in such distributed network/s.

The functional and structural connectivity may constrain the extent of potential networks and therefore shed light on the

cognitive characteristics of LS-VOT (e.g., Pessoa, 2014; Chen et al., 2019). The local or sparse connections with other brain areas will restrict the role of the region of interest. In the case of LS-VOT, a number of connections both structural and functional connections were found, with many distant regions within the language network, which exist even before the reading acquisition. According to the *biased connectivity hypothesis* (Dehaene and Dehaene-Lambertz, 2016; Moulton et al., 2019) the location of LS-VOT is directly determined by the structural connections to other cortical language areas.

The connectivity of LS-VOT with the language network was studied from the earliest stages of development. Li et al. (2020) studied newborns within 1 week after birth. They examined the resting state activity that showed significant connectivity between anterior LS-VOT and frontal and temporal language networks. Saygin et al. (2016) scanned 5-year-olds before they learned to read. At the age of eight children were tested again with tasks that determined the functional localization of VWFA. The VWFA area even before the reading acquisition had white matter (anatomical fiber tracts) connections with speech and language processing networks. Moulton et al. (2019) showed that microstructural changes in the pathway between LS-VOT and the left inferior parietal lobule (IPL) correlated with the reading level in the first year of reading instruction. Stevens et al. (2017) asked if the functional connectivity between VWFA and the language system is specifically tuned to processing words vs. other visual stimuli like namable pictures. They showed that resting-state connectivity of LS-VOT with the left posterior STG is preferential compared to other visual stimuli. Also, Bouhali et al. (2014) compared VWFA with the fusiform face area (FFA) and proved privileged connectivity for VWFA to left perisylvian superior temporal and inferior frontal areas (but for a domain-general view see: Vogel et al., 2013).

The interesting question in this field of research is how to explain the role of the preferential connectivity between some parts of VOT and the language network even before children start to read. The answer to this question might advance our knowledge of the VOT role in language processing in general. The simplest hypothesis is that connections between VOT and language systems are necessary for naming visual stimuli. Stevens et al. (2017) showed that in the semantic classification task (deciding whether the stimuli were man-made or natural objects), the connections between the left posterior STG and LS-VOT predicted only performance on word stimuli compared to picture stimuli. The authors proposed that while structural connectivity does not drive specialization, the experience-driven "coupling among regions critical for performance during skill acquisition" (p. 5296) leads to higher connectivity of those regions over time. However, longitudinal studies are needed since the preferential connectivity of LS-VOT with language networks in adults might be a result of reading training not a cause of LS-VOT engagement in reading.

The experience-driven hypothesis of the LS-VOT specialization for language is supported by the studies on the blind population. As mentioned before in the early and congenitally blind LS-VOT is engaged in speech processing on a higher level (e.g., in tasks demanding syntactic processing) than it is observed in the sighted population. According to the pluripotent cortex hypothesis (Bedny, 2017) such activity may be an effect of similar structural connectivity of the VOT with other brain regions but changed

experience, as no visual input enters this region in the blind. The connections with the language processing areas in this context may get strengthened (Abboud and Cohen, 2019; Kanjlia et al., 2021) and lead to increased sensitivity to language early on in the development of blind individuals. The LS-VOT would thus be a part of distributed, modality-independent language network (Dzięgiel-Fivet et al., 2021) even before reading acquisition and become specialized for Braille reading only afterward in a similar manner in which frontal and temporal areas become engaged in the visual reading. This hypothesis was further supported by the observation that in the blinds LS-VOT lacks the posterior-to-anterior organization gradient that is observed in the sighted (Tian et al., 2022). Instead, such a gradient can be observed in the modality-specific posterior-parietal cortex in the blind.

As for the comprehensive theory of the role of LS-VOT in a distributed system the most known Interactive Account was given by Price and Devlin (2011). According to their proposal, LS-VOT is not responsible for encoding orthographic or visual information but serves as an "interface" between sensory input and top-down predictions modulated by attentional and task requirements. In default "sensory inputs" are visual properties of words and "top-down predictions" correspond to the non-visual features of stimuli like phonological or semantic information. However, the authors see linguistic processing as a distributed system where it is difficult to dissociate the parts of cognitive functions that are implemented in a given region of the network. According to that view, "orthographic representations emerge from the interaction of backward and forward influences" (Price and Devlin, 2011, paragraph 3). The authors use a "prediction error" concept: it results from the top-down influence of linguistic information. Greater prediction error (mismatch between visual input and top-down predictions) evokes higher activity of the LS-VOT. This, according to the authors, explains why the LS-VOT activates more strongly for pseudowords than words: real words cause the lowest prediction error. This is an alternative explanation to the "Familiarity effect" (Kronbichler et al., 2004; discussed in paragraph 3) or "Rapid Adaptation effect" (Glezer et al., 2009, 2016) where the LS-VOT is less active on known stimuli because of the adaptation processes. However, the context (e.g., adding attentional demands) might change the activity pattern of the LS-VOT. In consequence, its activity should be disturbed and overall lower in reading deficit because linguistic top-down predictions are less precise. The developmental stage also matters: LS-VOT activity should be highest at the beginning of learning to read because top-down predictions are only starting to be formed. The preliminary empirical evidence was provided, e.g., by Wang et al. (2022): based on graph analysis results the authors claimed that the LS-VOT serves as an "interface" between visual and higher-order systems. In some tasks (sentence comprehension) LS-VOT becomes a connector in the auditory-sensorimotor system whereas in speech processing in noise when the signal is severely degraded LS-VOT serves as a peripheral part of a visual system.

White et al. (2023) also showed a task-dependent modulation of LS-VOT. In the case of processing written words, the task to recognize them (vs. ignoring them) resulted in an increased level of LS-VOT activity compared to processing symbol strings. The task-dependent modulation for words was associated with higher functional connectivity with language regions and was only visible in a part of LS-VOT that corresponds to VWFA but not in the overall visual cortex. It shows that the LS-VOT region is modulated

by the need for reading words but not processing other visual stimuli.

Another proposal suggesting that the LS-VOT is part of a distributed neural system was formulated by Chen et al. (2019). The authors showed results in favor of a multiplex model of LS-VOT. They examined structural connectivity between LS-VOT and *a priori* defined regions of the language and attention networks. LS-VOT showed an even stronger connection with the attention network (frontoparietal nodes) than with the language network. Also, the double dissociation in brain-behavior relation was discovered: the level of structural connectivity between the LS-VOT and nodes within the language network was found to be a predictor of individual differences in reading and language abilities, but not attention. Still the degree of structural connectivity between the LS-VOT and nodes in the dorsal frontoparietal attentional network was associated with visual attention abilities, but not with reading and language abilities. The results are particularly interesting in light of the discussion on the LS-VOT involvement in speech processing because most of the phonological tasks evoking activity of LS-VOT were attention-based (e.g., phoneme deletion or rhyme matching) compared to passive listening of speech. However, the multiplex model assumes interaction between attention and language in the left VOT – not necessarily two distinct roles of the left VOT. In general, thanks to the local connections with the visual system and distant relations with the attentional and language systems the left VOT is an "attentional spotlight" on word-like stimuli that are later processed in a language network. Woodhead et al. (2014) studied the role of the left IFG in word recognition. They found that the left IFG is sensitive to words and provides top-down feedback to the VOT, aiding in efficient word identification. This feedback occurs in the early stages of processing. In line with this highly interactive view, Ellenblum et al. (2019) showed that the orthographic network is not as coherent as other well-described networks (like DMN). The authors explained that the orthographic process requires highly specialized cross-domain and cross-modality interactions and many already complex cognitive functions therefore they point to the "high-level integrative" role of the LS-VOT in reading and spelling.

6. LS-VOT acquires its function in the development

Based on early connectivity studies of structural and functional connections of LS-VOT in childhood (as in e.g., Saygin et al., 2016) different developmental paths of LS-VOT involvement in reading and language processing might be formulated. The canonical approach comes from Dehaene, Cohen, and colleagues (e.g., Dehaene and Cohen, 2007) proposal that we may call here "the orthographic hypothesis." In this view, the development of orthographic sensitivity in LS-VOT, which is primarily responsible for complex visual stimuli processing, is driven by literacy development. Then possibly automatic orthographic co-activations grow during phonology processing, which makes LS-VOT sensitive to speech processing even without the visual stimuli present.

In detail, the original neuronal recycling hypothesis claims that when we learn to read, our brain repurposes certain areas of the left LS-VOT previously used for recognizing other things like faces or objects. The process of neuronal recycling would

involve a competition in which the group of neurons used in print processing "invades" the regions of the LS-VOT and takes them over for reading (Dehaene and Cohen, 2007). The hypothesis has been prominent since it was proposed and referenced in studies on both adults (Dehaene et al., 2010; Pegado et al., 2014) and children (Monzalvo and Dehaene-Lambertz, 2013). Studies comparing literate and illiterate adults have found that LS-VOT regions involved in reading also respond to other visual stimuli like objects, faces, and checkerboards. As reading ability improved, responses to faces decreased slightly in the left side of the brain and increased significantly in the right side (Dehaene et al., 2010; Pegado et al., 2014). Similarly in children, right lateralization of the activation to faces in the VOT increased with reading performance (Monzalvo et al., 2012). More recently, also a "weaker" or "revised" version of the hypothesis has been proposed, based on the longitudinal data (Dehaene-Lambertz et al., 2018). The revised hypothesis suggests that the brain has dedicated areas for processing different visual categories, which expand as we grow. With reading instruction, the LS-VOT responds to written words at initially weakly specialized sites, and without altering their (weak) preexisting responsivity to other visual inputs, such as faces. This view was also supported by recent studies that reported co-existence of growing word sensitivity and other visual categories representations (Nordt et al., 2021; Feng et al., 2022; Chyl et al., 2023).

Nonetheless, the relationship between the emergence of different visual categories and competition in the LS-VOT is currently far from being a consensus, and the hypothesis has been critically discussed. New research has found that literacy can actually enhance the similarity between representations of text and faces, without reducing the response to other, non-linguistic visual categories (Hervais-Adelman et al., 2019; Van Paridon et al., 2021). In fact, the recent critical review (Rossion and Lochy, 2022) found little evidence to support the idea that reading ability affects the way the brain processes faces. Instead, the review argued that right-lateralized neural activity for face recognition emerges early in life, and is not modulated by literacy level. Therefore, it is hard to say what is actually "recycled" if word selectivity invades cortical regions that are not selective (or weakly selective) to faces or other categories, as the "revised" version of the hypothesis postulates. Hence, the authors suggest abandoning the misleading "recycling" terminology altogether, not just "revising" it (Rossion and Lochy, 2022). They propose the term "neural competition" in which sensory inputs sharing functional characteristics (e.g., faces and words) compete for the same population of neurons within the left VOT. Also, Vogel et al. (2012) 2014 studies on adults showed that the acquisition of lexical representations does not necessarily replace the ability of LS-VOT for visual analysis. Instead this region remains crucial for reading thanks to its sensitivity to visual characteristics of print and its involvement in statistical learning that enables fluent processing of real words. However, the same region might be useful for processing other types of information.

The alternative pathway of LS-VOT functional development might be called "the phonology to orthography hypothesis." This alternative was formulated by Conant et al. (2020) who claimed that areas within VOT are involved in speech-face circuitry because of the proximity to FFA. After reading acquisition, some parts of LS-VOT that were involved in processing speech become responsible for audiovisual integration between phonology and orthography

and later LS-VOT starts to be responsible for processing unimodal orthographical forms. This alternative explains what might be the evolutionary relevant function of the connections between some parts of the VOT and the language networks before reading acquisition. If this is the case, the preferential activity for speech sounds in LS-VOT should be observed already in small children before schooling. So far, there is evidence of LS-VOT involvement in phonological processing at the beginning of reading acquisition but not in true pre-readers without any experience with print or letter knowledge. For example, Dębska et al. (2016) showed stronger LS-VOT involvement in 6–7 years old Polish children in an auditory rhyming task in a group without the familial risk for dyslexia compared to the risk group. Similarly, Wang J. et al. (2018) showed that activity of the posterior left VOT correlated with a reading level in an auditory onset comparison task in 5–6 years old beginning readers in English. Also, the activity of the posterior left VOT was related to efficiency in a phonological in-scanner task. However, Dehaene et al., (2010, 2015) claimed that LS-VOT is not sensitive to speech or phonology in illiterate adults. Therefore more evidence on preliterate children is needed to prove the preferential engagement of LS-VOT in speech processing.

Another promising but less studied explanation is "the growing multimodality hypothesis." First, the sensitivity for orthography in LS-VOT might be explained to be a consequence of a multimodal interaction during establishing letter–speech sound correspondences (Brem et al., 2010). This recurring co-activation in the reading process might lead to establishing an ortho-phonological representation based on connectivity with a speech processing network in the left STG. In this view, there are no "pure" orthographic representations that are not related to phonology – at least in a typical development of reading. Analogically the constant co-activation may lead to the restructuring of primary phonological areas like the left STG in a way that this region becomes sensitive to strictly orthographic effects like consistency in spelling (as proposed by Pattamadilok et al., 2010).

7. Conclusion

The research described in this article provides evidence that the term "Visual Word Form Area" is insufficient to describe the cognitive role of the language specific - VOT (LS-VOT) area. Different phonological, orthographic, and semantic functions of the LS-VOT were found that turned out to be independent of modality. The most promising approach for defining a general cognitive function of the LS-VOT seems to be focusing on its preferential structural and functional connectivity with higher-level language and attention networks. In this view, the LS-VOT may be described as a task-driven "interactive gateway" that connects certain modality-independent stimuli with their associated orthographic, semantic, and phonological properties processed within the whole network. The activity of the LS-VOT is not limited to a specific script or orthography system but extends to all symbolic communication-relevant stimuli that convey meaning in a repeatable manner.

Overall the ventral visual pathway may play a more major role as an interactive hub connecting modality-independent experience with brain regions specialized for different functions. The shift toward a domain-general perspective in understanding

the functions of the ventral stream is visible in studies on processing numbers (Chen and Verguts, 2012, 2017; Grotheer et al., 2019). Specialization in the ventral "visual" stream can develop regardless of sensory modality or visual experience (Abboud et al., 2015; Grotheer et al., 2016). This phenomenon occurs due to unique patterns of connectivity (Grotheer et al., 2019). Similar findings have been observed in studies on action-object recognition, categorization processes (Grill-Spector et al., 2001; Mahon et al., 2007, 2009) and semantic representations (Chen and Mirman, 2015). A crucial area of focus for future research is to determine whether the functional connectivity between the ventral stream and other structures beyond it serves as a fundamental organizing principle that leads to category-specific processing in the human visual system.

Author contributions

AD contributed to the conceptualization and wrote the first draft of the manuscript. MW, KC, and GD-F wrote sections of the manuscript. KC prepared the figures. KJ revised the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

References

Abboud, S., and Cohen, L. (2019). Distinctive interaction between cognitive networks and the visual cortex in early blind individuals. *Cereb. Cortex* 29, 4725–4742.

Abboud, S., Maidenbaum, S., Dehaene, S., and Amedi, A. (2015). A number-form area in the blind. *Nat. Commun.* 6:6026.

Amedi, A., Hofstetter, S., Maidenbaum, S., and Heimler, B. (2017). Task selectivity as a comprehensive principle for brain organization. *Trends Cogn. Sci.* 21, 307–310.

Amedi, A., Raz, N., Pianka, P., Malach, R., and Zohary, E. (2003). Early 'visual' cortex activation correlates with superior verbal memory performance in the blind. *Nat. Neurosci.* 6, 758–766. doi: 10.1038/nn1072

Arnaud, L., Sato, M., Ménard, L., and Gracco, V. L. (2013). Repetition suppression for speech processing in the associative occipital and parietal cortex of congenitally blind adults. *PLoS One* 8:e64553. doi: 10.1371/journal.pone.0064553

Bai, J. E., Shi, J., Jiang, Y., He, S., and Weng, X. (2011). Chinese and Korean characters engage the same visual word form area in proficient early Chinese-Korean bilinguals. *PLoS One* 6:e22765. doi: 10.1371/journal.pone.0022765

Bedny, M. (2017). Evidence from blindness for a cognitively pluripotent cortex. *Trends Cogn. Sci.* 21, 637–648. doi: 10.1016/j.tics.2017.06.003

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. doi: 10.1016/j.neuroimage.2006.06.053

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, J. R., Burman, D. D., Meyer, J. R., Gitelman, D. R., Parrish, T. B., and Mesulam, M. M. (2002). Functional anatomy of intra-and cross-modal lexical tasks. *Neuroimage* 16, 7–22. doi: 10.1006/nimg.2002.1081

Bouhali, F., de Schotten, M. T., Pinel, P., Poupon, C., Mangin, J. F., Dehaene, S., et al. (2014). Anatomical connections of the visual word form area. *J. Neurosci.* 34, 15402–15414.

Brem, S., Bach, S., Kucian, K., Kujala, J. V., Guttorm, T. K., Martin, E., et al. (2010). Brain sensitivity to print emerges when children learn letter–speech sound correspondences. *Proc. Natl. Acad. Sci. U. S. A.* 107, 7939–7944.

Bruno, J. L., Zumberge, A., Manis, F. R., Lu, Z. L., and Goldman, J. G. (2008). Sensitivity to orthographic familiarity in the occipito-temporal region. *Neuroimage* 39, 1988–2001.

Büchel, C., Price, C., Frackowiak, R. S., and Friston, K. (1998a). Different activation patterns in the visual cortex of late and congenitally blind individuals. *Brain* 121, 409–419. doi: 10.1093/brain/121.3.409

Büchel, C., Price, C., and Friston, K. (1998b). A multimodal language region in the ventral visual pathway. *Nature* 394, 274–277. doi: 10.1038/28389

Burton, H., Diamond, J. B., and McDermott, K. B. (2003). Dissociating cortical regions activated by semantic and phonological tasks: a FMRI study in blind and sighted people. *J. Neurophysiol.* 90, 1965–1982. doi: 10.1152/jn.00279.2003

Burton, H., Snyder, A. Z., Conturo, T. E., Akbudak, E., Ollinger, J. M., and Raichle, M. E. (2002). Adaptive changes in early and late blind: a fMRI study of Braille reading. *J. Neurophysiol.* 87, 589–607. doi: 10.1152/jn.00285.2001

Carlos, B. J., Hirshorn, E. A., Durisko, C., Fiez, J. A., and Coutanche, M. N. (2019). Word inversion sensitivity as a marker of visual word form area lateralization: An application of a novel multivariate measure of laterality. *Neuroimage* 191, 493–502. doi: 10.1016/j.neuroimage.2019.02.044

Chao, L. L., Weisberg, J., and Martin, A. (2002). Experience-dependent modulation of category-related cortical activity. *Cereb. Cortex* 12, 545–551. doi: 10.1093/cercor/12.5.545

Chen, L., Wassermann, D., Abrams, D. A., Kochalka, J., Gallardo-Diez, G., and Menon, V. (2019). The visual word form area (VWFA) is part of both language and attention circuitry. *Nat. Commun.* 10, 5601. doi: 10.1038/s41467-019-13634-z

Chen, Q., and Mirman, D. (2015). Interaction between phonological and semantic representations: Time matters. *Cogn. Sci.* 39, 538–558. doi: 10.1111/cogs.12156

Chen, Q., and Verguts, T. (2012). Spatial intuition in elementary arithmetic: a neurocomputational account. *PLoS One* 7:e31180. doi: 10.1371/journal.pone.0031180

Chen, Q., and Verguts, T. (2017). Numerical Proportion Representation: A Neurocomputational Account. *Front. Hum. Neurosci.* 11:412. doi: 10.3389/fnhum.2017.00412

Chyl, K., Kossowski, B., Wang, S., Dębska, A., Łuniewska, M., Marchewka, A., et al. (2021). The brain signature of emerging reading in two contrasting languages. *NeuroImage* 225:117503.

Chyl, K., Gentile, F., Dębska, A., Dynak, A., Łuniewska, M., Wójcik, M., et al. (2023). Early reading skills and the ventral occipito-temporal cortex organization. *Cortex* 160, 134–151. doi: 10.1016/j.cortex.2023.01.004

Chyl, K., Kossowski, B., Dębska, A., Łuniewska, M., Banaszkiewicz, A., Żelechowska, A., et al. (2018). Prereader to beginning reader: changes induced by reading acquisition

in print and speech brain networks. *J. Child Psychol. Psychiatry* 59, 76–87. doi: 10.1111/jcpp.12774

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M. A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal individuals and posterior split-brain patients. *Brain* 123, 291–307.

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. doi: 10.1016/j.neuroimage.2004.07.052

Cohen, L., Lehéricy, 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. doi: 10.1093/brain/awf094

Conant, L. L., Liebenthal, E., Desai, A., and Binder, J. R. (2014). FMRI of phonemic perception and its relationship to reading development in elementary-to middle-school-age children. *Neuroimage* 89, 192–202. doi: 10.1016/j.neuroimage.2013.11.055

Conant, L. L., Liebenthal, E., Desai, A., Seidenberg, M. S., and Binder, J. R. (2020). Differential activation of the visual word form area during auditory phoneme perception in youth with dyslexia. *Neuropsychologia* 146:107543. doi: 10.1016/j.neuropsychologia.2020.107543

Dębska, A., Chyl, K., Dzięgiel, G., Kacprzak, A., Łuniewska, M., Plewko, J., et al. (2019). Reading and spelling skills are differentially related to phonological processing: Behavioral and fMRI study. *Dev. Cogn. Neurosci.* 39:100683. doi: 10.1016/j.dcn.2019.100683

Dębska, A., Łuniewska, M., Chyl, K., Banaszkiewicz, A., Żelechowska, A., Wypych, M., et al. (2016). Neural basis of phonological awareness in beginning readers with familial risk of dyslexia—Results from shallow orthography. *NeuroImage* 132, 406–416. doi: 10.1016/j.neuroimage.2016.02.063

Dehaene, S., and Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron* 56, 384–398.

Dehaene, S., and Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends Cogn. Sci.* 15, 254–262.

Dehaene, S., Cohen, L., Morais, J., and Kolinsky, R. (2015). Illiterate to literate: Behavioural and cerebral changes induced by reading acquisition. *Nat. Rev. Neurosci.* 16, 234–244. doi: 10.1038/nrn3924

Dehaene, S., Cohen, L., Sigman, M., and Vinckier, F. (2005). The neural code for written words: a proposal. *Trends Cogn. Sci.* 9, 335–341. doi: 10.1016/j.tics.2005.05.004

Dehaene, S., and Dehaene-Lambertz, G. (2016). Is the brain prewired for letters? *Nat. Neurosci.* 19, 1192–1193. doi: 10.1038/nn.4369

Dehaene, S., Pegado, F., Braga, L., Ventura, P., Filho, G., Jobert, A., et al. (2010). How learning to read changes the cortical networks for vision and language. *Science* 330, 1359–1364.

Dehaene-Lambertz, G., Monzalvo, K., and Dehaene, S. (2018). The emergence of the visual word form: Longitudinal evolution of category-specific ventral visual areas during reading acquisition. *PLoS Biol.* 16:e2004103. doi: 10.1371/journal.pbio.2004103

Desroches, A. S., Cone, N. E., Bolger, D. J., Bitan, T., Burman, D. D., and Booth, J. R. (2010). Children with reading difficulties show differences in brain regions associated with orthographic processing during spoken language processing. *Brain Res.* 1356, 73–84. doi: 10.1016/j.brainres.2010.07.097

Dzięgiel-Fivet, G., Plewko, J., Szczerbiński, M., Marchewka, A., Szwed, M., and Jednoróg, K. (2021). Neural network for Braille reading and the speech-reading convergence in the blind: Similarities and differences to visual reading. *NeuroImage* 231:117851. doi: 10.1016/j.neuroimage.2021.117851

Ellenblum, G., Purcell, J. J., Song, X., and Rapp, B. (2019). High-level integrative networks: a resting-state fMRI investigation of reading and spelling. *J. Cogn. Neurosci.* 31, 961–977. doi: 10.1162/jocn_a_01405

Feng, X., Altarelli, I., Monzalvo, K., Ding, G., Ramus, F., Shu, H., et al. (2021). A universal reading network and its modulation by writing system and reading ability in French and Chinese children. *eLife* 9:e54591. doi: 10.7554/eLife.54591

Feng, X., Monzalvo, K., Dehaene, S., and Dehaene-Lambertz, G. (2022). Evolution of reading and face circuits during the first three years of reading acquisition. *Neuroimage* 259:119394. doi: 10.1016/j.neuroimage.2022.119394

Fischer-Baum, S., Bruggemann, D., Gallego, I. F., Li, D. S., and Tamez, E. R. (2017). Decoding levels of representation in reading: A representational similarity approach. *Cortex* 90, 88–102. doi: 10.1016/j.cortex.2017.02.017

Frost, S. J., Landi, N., Mencl, W. E., Sandak, R., Fulbright, R. K., Tejada, E. T., et al. (2009). Phonological awareness predicts activation patterns for print and speech. *Ann. Dyslexia* 59, 78–97. doi: 10.1007/s11881-009-0024-y

Gao, X., Gentile, F., and Rossion, B. (2018). Fast periodic stimulation (FPS): a highly effective approach in fMRI brain mapping. *Brain Struct. Funct.* 223, 2433–2454. doi: 10.1007/s00429-018-1630-4

Glezer, L. S., Eden, G., Jiang, X., Luetje, M., Napoliello, E., Kim, J., et al. (2016). Uncovering phonological and orthographic selectivity across the reading network using fMRI-RA. *Neuroimage* 138, 248–256. doi: 10.1016/j.neuroimage.2016.05.072

Glezer, L. S., Jiang, X., and Riesenhuber, M. (2009). Evidence for highly selective neuronal tuning to whole words in the 'visual word form area'. *Neuron* 62, 199–204. doi: 10.1016/j.neuron.2009.03.017

Glezer, L. S., Kim, J., Rule, J., Jiang, X., and Riesenhuber, M. (2015). Adding words to the brain's visual dictionary: novel word learning selectively sharpens orthographic representations in the VWFA. *J. Neurosci.* 35, 4965–4972. doi: 10.1523/JNEUROSCI.4031-14.2015

Grill-Spector, K., Kourtzi, Z., and Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vis. Res.* 41, 1409–1422.

Grill-Spector, K., and Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol.* 107, 293–321. doi: 10.1016/s0001-6918(01)00019-1

Grotheer, M., Ambrus, G. G., and Kovács, G. (2016). Causal evidence of the involvement of the number form area in the visual detection of numbers and letters. *Neuroimage* 132, 314–319. doi: 10.1016/j.neuroimage.2016.02.069

Grotheer, M., Zhen, Z., Lerma-Usabiaga, G., and Grill-Spector, K. (2019). Separate lanes for adding and reading in the white matter highways of the human brain. *Nat. Commun.* 10:3675. doi: 10.1038/s41467-019-11424-1

Hashimoto, R., and Sakai, K. L. (2004). Learning letters in adulthood: direct visualization of cortical plasticity for forming a new link between orthography and phonology. *Neuron* 42, 311–322. doi: 10.1016/s0896-6273(04)00196-5

Hervais-Adelman, A., Kumar, U., Mishra, R. K., Tripathi, V. N., Guleria, A., Singh, J. P., et al. (2019). Learning to read recycles visual cortical networks without destruction. *Sci. Adv.* 5, eaax0262.

Hirshorn, E. A., and Harris, L. N. (2022). Culture is not destiny, for reading: highlighting variable routes to literacy within writing systems. *Ann. N. Y. Acad. Sci.* 1513, 31–47.

Hirshorn, E. A., Li, Y., Ward, M. J., Richardson, R. M., Fiez, J. A., and Ghuman, A. S. (2016). Decoding and disrupting left midfusiform gyrus activity during word reading. *Proc. Natl. Acad. Sci. U. S. A.* 113, 8162–8167. doi: 10.1073/pnas.1604126113

Hodgson, V. J., Ralph, M. A. L., and Jackson, R. L. (2021). Multiple dimensions underlying the functional organization of the language network. *Neuroimage* 241:118444.

Hsiao, J. H., and Lam, S. M. (2013). The modulation of visual and task characteristics of a writing system on hemispheric lateralization in visual word recognition—A computational exploration. *Cogn. Sci.* 37, 861–890. doi: 10.1111/cogs.12033

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. doi: 10.1016/S1053-8119(03)00343-4

Kanjlia, S., Loiotile, R. E., Harhen, N., and Bedny, M. (2021). 'Visual' cortices of congenitally blind adults are sensitive to response selection demands in a go/no-go task. *NeuroImage* 236:118023. doi: 10.1016/j.neuroimage.2021.118023

Kay, K. N., and Yeatman, J. D. (2017). Bottom-up and top-down computations in word-and face-selective cortex. *eLife* 6:e22341. doi: 10.7554/eLife.22341

Kim, J. S., Kanjlia, S., Merabet, L. B., and Bedny, M. (2017). Development of the visual word form area requires visual experience: Evidence from blind braille readers. *J. Neurosci.* 37, 11495–11504. doi: 10.1523/JNEUROSCI.0997-17.2017

Krafnick, A. J., Tan, L. H., Flowers, D. L., Luetje, M. M., Napoliello, E. M., Siok, W. T., et al. (2016). Chinese character and English word processing in children's ventral occipitotemporal cortex: fMRI evidence for script invariance. *Neuroimage* 133, 302–312. doi: 10.1016/j.neuroimage.2016.03.021

Kronbichler, M., Bergmann, J., Hutzler, F., Staffen, W., Mair, A., Ladurner, G., et al. (2007). Taxi vs. Taksi: Orthographic word recognition in the left ventral occipitotemporal cortex. *J. Cogn. Neurosci.* 19, 1584–1594. doi: 10.1162/jocn.2007.19.10.1584

Kronbichler, M., Hutzler, F., Wimmer, H., Mair, A., Staffen, W., and Ladurner, G. (2004). The visual word form area and the frequency with which words are encountered: evidence from a parametric fMRI study. *Neuroimage* 21, 946–953. doi: 10.1016/j.neuroimage.2003.10.021

Lerma-Usabiaga, G., Carreiras, M., and Paz-Alonso, P. M. (2018). Converging evidence for functional and structural segregation within the left ventral occipitotemporal cortex in reading. *Proc. Natl. Acad. Sci. U.S.A.* 115, E9981–E9990. doi: 10.1073/pnas.1803003115

Li, J., Osher, D. E., Hansen, H. A., and Saygin, Z. M. (2020). Innate connectivity patterns drive the development of the visual word form area. *Sci. Rep.* 10:18039. doi: 10.1038/s41598-020-75015-7

Li, Y., Zhang, L., Xia, Z., Yang, J., Shu, H., and Li, P. (2017). The relationship between intrinsic couplings of the visual word form area with spoken language network and reading ability in children and adults. *Front. Hum. Neurosci.* 11:327. doi: 10.3389/fnhum.2017.00327

Liberman, A. M. (1992). "The relation of speech to reading and writing," in *Advances in Psychology*, eds R. Frost and L. Katz (North-Holland: American Psychological Association).

Liu, C., Zhang, W. T., Tang, Y. Y., Mai, X. Q., Chen, H. C., Tardif, T., et al. (2008). The visual word form area: evidence from an fMRI study of implicit processing of Chinese characters. *Neuroimage* 40, 1350–1361. doi: 10.1016/j.neuroimage.2007.10.014

Ludersdorfer, P., Kronbichler, M., and Wimmer, H. (2015). Accessing orthographic representations from speech: The role of left ventral occipitotemporal cortex in spelling. *Hum. Brain Mapp.* 36, 1393–1406. doi: 10.1002/hbm.22709

Ludersdorfer, P., Schurz, M., Richlan, F., Kronbichler, M., and Wimmer, H. (2013). Opposite effects of visual and auditory word-likeness on activity in the visual word form area. *Front. Hum. Neurosci.* 7:491. doi: 10.3389/fnhum.2013.00491

Ludersdorfer, P., Wimmer, H., Richlan, F., Schurz, M., Hutzler, F., and Kronbichler, M. (2016). Left ventral occipitotemporal activation during orthographic and semantic processing of auditory words. *Neuroimage* 124, 834–842.

Mahon, B. Z., Anzellotti, S., Schwarzbach, J., Zampini, M., and Caramazza, A. (2009). Category-specific organization in the human brain does not require visual experience. *Neuron* 63, 397–405.

Mahon, B. Z., Milleville, S. C., Negri, G. A., Rumiati, R. I., Caramazza, A., and Martin, A. (2007). Action-related properties shape object representations in the ventral stream. *Neuron* 55, 507–520. doi: 10.1016/j.neuron.2007.07.011

Marks, R. A., Kovelman, I., Kepinska, O., Oliver, M., Xia, Z., Haft, S. L., et al. (2019). Spoken language proficiency predicts print-speech convergence in beginning readers. *NeuroImage* 201:116021. doi: 10.1016/j.neuroimage.2019.116021

McCandliss, B. D., Cohen, L., and Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends Cogn. Sci.* 7, 293–299. doi: 10.1016/S1364-6613(03)00134-7

McNorgan, C., and Booth, J. R. (2015). Skill dependent audiovisual integration in the fusiform induces repetition suppression. *Brain Lang.* 141, 110–123. doi: 10.1016/j.bandl.2014.12.002

Monzalvo, K., and Dehaene-Lambertz, G. (2013). How reading acquisition changes children's spoken language network. *Brain Lang.* 127, 356–365. doi: 10.1016/j.bandl.2013.10.009

Monzalvo, K., Fluss, J., Billard, C., Dehaene, S., and Dehaene-Lambertz, G. (2012). Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status. *Neuroimage* 61, 258–274. doi: 10.1016/j.neuroimage.2012.02.035

Morais, J., Cary, L., Alegria, J., and Bertelson, P. (1979). Does awareness of speech as a sequence of phones arise spontaneously? *Cognition* 7, 323–331.

Morken, F., Helland, T., Hugdahl, K., and Specht, K. (2017). Reading in dyslexia across literacy development: A longitudinal study of effective connectivity. *Neuroimage* 144, 92–100. doi: 10.1016/j.neuroimage.2016.09.060

Moulton, E., Bouhali, F., Monzalvo, K., Poupon, C., Zhang, H., Dehaene, S., et al. (2019). Connectivity between the visual word form area and the parietal lobe improves after the first year of reading instruction: a longitudinal MRI study in children. *Brain Struct. Funct.* 224, 1519–1536. doi: 10.1007/s00429-019-01855-3

Nestor, A., Behrmann, M., and Plaut, D. C. (2013). The neural basis of visual word form processing: a multivariate investigation. *Cereb. Cortex* 23, 1673–1684. doi: 10.1093/cercor/bhs158

Neudorf, J., Gould, L., Mickleborough, M. J., Ekstrand, C., and Borowsky, R. (2022). Unique, shared, and dominant brain activation in visual word form area and lateral occipital complex during reading and picture naming. *Neuroscience* 481, 178–196. doi: 10.1016/j.neuroscience.2021.11.022

Nordt, M., Gomez, J., Natu, V. S., Rezai, A. A., Finzi, D., Kular, H., et al. (2021). Cortical recycling in high-level visual cortex during childhood development. *Nat. Hum. Behav.* 5, 1686–1697. doi: 10.1038/s41562-021-01141-5

Pattamadilok, C., Knierim, I., Duncan, K. K., and Devlin, J. T. (2009). "Neural mechanism underlying orthographic influence on speech processing: A combined TMS and behaviour study," in *Proceedings of the 16th Annual Meeting of the Cognitive Neuroscience Society*, London.

Pattamadilok, C., Knierim, I. N., Duncan, K. J. K., and Devlin, J. T. (2010). How does learning to read affect speech perception? *J. Neurosci.* 30, 8435–8444.

Pattamadilok, C., Planton, S., and Bonnard, M. (2019). Spoken language coding neurons in the Visual Word Form Area: Evidence from a TMS adaptation paradigm. *NeuroImage* 186, 278–285. doi: 10.1016/j.neuroimage.2018.11.014

Pegado, F., Comerlato, E., Ventura, F., Jobert, A., Nakamura, K., Buiatti, M., et al. (2014). Timing the impact of literacy on visual processing. *Proc. Natl. Acad. Sci. U. S. A.* 111, E5233–E5242. doi: 10.1073/pnas.1417347111

Planton, S., Chanoine, V., Sein, J., Anton, J. L., Nazarian, B., Pallier, C., et al. (2019). Top-down activation of the visuo-orthographic system during spoken sentence processing. *Neuroimage* 202:116135. doi: 10.1016/j.neuroimage.2019.116135

Pessoa, L. (2014). Understanding brain networks and brain organization. *Phys. Life Rev.* 11, 400–435.

Preston, J. L., Molfese, P. J., Frost, S. J., Mencl, W. E., Fulbright, R. K., Hoeft, F., et al. (2016). Print-speech convergence predicts future reading outcomes in early readers. *Psychol. Sci.* 27, 75–84. doi: 10.1177/0956797615611921

Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *Neuroimage* 62, 816–847. doi: 10.1016/j.neuroimage.2012.04.062

Price, C. J., and Devlin, J. T. (2003). The myth of the visual word form area. *Neuroimage* 19, 473–481. doi: 10.1016/s1053-8119(03)00084-3

Price, C. J., and Devlin, J. T. (2011). The interactive account of ventral occipitotemporal contributions to reading. *Trends Cogn. Sci.* 15, 246–253.

Pylkkänen, L., and Okano, K. (2010). The nature of abstract orthographic codes: Evidence from masked priming and magnetoencephalography. *PLoS One* 5:e10793. doi: 10.1371/journal.pone.0010793

Qu, J., Pang, Y., Liu, X., Cao, Y., Huang, C., and Mei, L. (2022). Task modulates the orthographic and phonological representations in the bilateral ventral Occipitotemporal cortex. *Brain Imag. Behav.* 16, 1695–1707. doi: 10.1007/s11682-022-00641-w

Rączy, K., Urbańczyk, A., Korczyk, M., Szewczyk, J., Sumera, E., and Szwed, M. (2019). Orthographic Priming in Braille Reading as Evidence for Task-specific Reorganization in the Ventral Visual Cortex of the Congenitally Blind. *J. Cogn. Neurosci.* 31, 1065–1078. doi: 10.1162/jocn_a_01407

Rapp, B., and Fischer-Baum, S. (2014). "Representation of orthographic knowledge," in *Oxford handbook of language production*, eds M. A. Goldrick, V. Ferreria, and M. Miozzo (New York, NY: Oxford University Press), 338–357.

Reich, L., Szwed, M., Cohen, L., and Amedi, A. (2011). A ventral visual stream reading center independent of visual experience. *Curr. Biol.* 21, 363–368. doi: 10.1016/j.cub.2011.01.040

Romanovska, L., Janssen, R., and Bonte, M. (2021). Cortical responses to letters and ambiguous speech vary with reading skills in dyslexic and typically reading children. *NeuroImage* 30:102588. doi: 10.1016/j.nicl.2021.102588

Rossion, B., and Lochy, A. (2022). Is human face recognition lateralized to the right hemisphere due to neural competition with left-lateralized visual word recognition? A critical review. *Brain Struct. Funct.* 227, 599–629. doi: 10.1007/s00429-021-02370-0

Roy, A. (2017). The theory of localist representation and of a purely abstract cognitive system: The evidence from cortical columns, category cells, and multisensory neurons. *Front. Psychol.* 8:186. doi: 10.3389/fpsyg.2017.00186

Rueckl, J. G., Paz-Alonso, P. M., Molfese, P. J., Kuo, W. J., Bick, A., Frost, S. J., et al. (2015). Universal brain signature of proficient reading: Evidence from four contrasting languages. *Proc. Natl. Acad. Sci. U. S. A.* 112, 15510–15515. doi: 10.1073/pnas.1509321112

Saygin, Z. M., Osher, D. E., Norton, E. S., Youssoufian, D. A., Beach, S. D., Feather, J., et al. (2016). Connectivity precedes function in the development of the visual word form area. *Nat. Neurosci.* 19, 1250–1255. doi: 10.1038/nn.4354

Schurz, M., Sturm, D., Richlan, F., Kronbichler, M., Ladurner, G., and Wimmer, H. (2010). A dual-route perspective on brain activation in response to visual words: evidence for a length by lexicality interaction in the visual word form area (VWFA). *Neuroimage* 49, 2649–2661. doi: 10.1016/j.neuroimage.2009.10.082

Sebastian, R., Gomez, Y., Leigh, R., Davis, C., Newhart, M., and Hillis, A. E. (2014). The roles of occipitotemporal cortex in reading, spelling, and naming. *Cogn. Neuropsychol.* 31, 511–528.

Siuda-Krzywicka, K., Bola, Ł, Paplińska, M., Sumera, E., Jednoróg, K., Marchewka, A., et al. (2016). Massive cortical reorganization in sighted Braille readers. *eLife* 5:e10762. doi: 10.7554/eLife.10762

Smith, G. J., Booth, J. R., and McNorgan, C. (2018). Longitudinal task-related functional connectivity changes predict reading development. *Front. Psychol.* 9:1754. doi: 10.3389/fpsyg.2018.01754

Song, Y., Tian, M., and Liu, J. (2012). Top-down processing of symbolic meanings modulates the visual word form area. *J. Neurosci.* 32, 12277–12283. doi: 10.1523/JNEUROSCI.1874-12.2012

Stevens, W. D., Kravitz, D. J., Peng, C. S., Tessler, M. H., and Martin, A. (2017). Privileged functional connectivity between the visual word form area and the language system. *J. Neurosci.* 37, 5288–5297. doi: 10.1523/JNEUROSCI.0138-17.2017

Szwed, M., Dehaene, S., Kleinschmidt, A., Eger, E., Valabrègue, R., Amadon, A., et al. (2011). Specialization for written words over objects in the visual cortex. *Neuroimage* 56, 330–344.

Thesen, T., McDonald, C. R., Carlson, C., Doyle, W., Cash, S., Sherfey, J., et al. (2012). Sequential then interactive processing of letters and words in the left fusiform gyrus. *Nat. Commun.* 3:1284. doi: 10.1038/ncomms2220

Tian, M., Saccone, E. J., Kim, J. S., Kanjlia, S., and Bedny, M. (2022). Sensory modality and spoken language shape reading network in blind readers of Braille. *Cereb. Cortex* 33, 2426–2440. doi: 10.1093/cercor/bhac216

Tong, F., and Pratte, M. S. (2012). Decoding patterns of human brain activity. *Annu. Rev. Psychol.* 63, 483–509.

Tylén, K., Wallentin, M., and Roepstorff, A. (2009). Say it with flowers! An fMRI study of object mediated communication. *Brain Lang.* 108, 159–166. doi: 10.1016/j.bandl.2008.07.002

Van Paridon, J., Ostarek, M., Arunkumar, M., and Huettig, F. (2021). Does neuronal recycling result in destructive competition? The influence of learning to read on the recognition of faces. *Psychol. Sci.* 32, 459–465. doi: 10.1177/0956797620971652

Van Turennout, M., Bielamowicz, L., and Martin, A. (2003). Modulation of neural activity during object naming: effects of time and practice. *Cereb. Cortex* 13, 381–391. doi: 10.1093/cercor/13.4.381

Vanderauwera, J., De Vos, A., Forkel, S. J., Catani, M., Wouters, J., Vandermosten, M., et al. (2018). Neural organization of ventral white matter tracts parallels the initial

steps of reading development: a DTI tractography study. *Brain Lang.* 183, 32–40. doi: 10.1016/j.bandl.2018.05.007

Ventura, P., Morais, J., and Kolinsky, R. (2007). The development of the orthographic consistency effect in speech recognition: From sublexical to lexical involvement. *Cognition* 105, 547–576. doi: 10.1016/j.cognition.2006.12.005

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. doi: 10.1016/j.neuron.2007.05.031

Vingerhoets, G., Alderweireldt, A. S., Vandemaele, P., Cai, Q., Van der Haegen, L., Brysbaert, M., et al. (2013). Praxis and language are linked: evidence from co-lateralization in individuals with atypical language dominance. *Cortex* 49, 172–118. doi: 10.1016/j.cortex.2011.11.003

Vogel, A. C., Church, J. A., Power, J. D., Miezin, F. M., Petersen, S. E., and Schlaggar, B. L. (2013). Functional network architecture of reading-related regions across development. *Brain Lang.* 125, 231–243. doi: 10.1016/j.bandl.2012.12.016

Vogel, A. C., Petersen, S. E., and Schlaggar, B. L. (2012). The left occipitotemporal cortex does not show preferential activity for words. *Cereb. Cortex* 22, 2715–2732.

Vogel, A. C., Petersen, S. E., and Schlaggar, B. L. (2014). The VWFA: it's not just for words anymore. *Front. Hum. Neurosci.* 8:88. doi: 10.3389/fnhum.2014.00088

Wang, J., Joanisse, M. F., and Booth, J. R. (2018). Reading skill related to left ventral occipitotemporal cortex during a phonological awareness task in 5–6 year old children. *Dev. Cogn. Neurosci.* 30, 116–122. doi: 10.1016/j.dcn.2018.01.011

Wang, X., Xu, Y., Wang, Y., Zeng, Y., Zhang, J., Ling, Z., et al. (2018). Representational similarity analysis reveals task-dependent semantic influence of the visual word form area. *Sci. Rep.* 8, 1–10. doi: 10.1038/s41598-018-21062-0

Wang, J., Joanisse, M. F., and Booth, J. R. (2021). Letter fluency in 7-8-year-old children is related to the anterior, but not posterior, ventral occipito-temporal cortex during an auditory phonological task. *Dev. Cogn. Neurosci.* 47:100898. doi: 10.1016/j.dcn.2020.100898

Wang, S., Planton, S., Chanoine, V., Sein, J., Anton, J. L., Nazarian, B., et al. (2022). Graph theoretical analysis reveals the functional role of the left ventral occipito-temporal cortex in speech processing. *Sci. Rep.* 12:20028. doi: 10.1038/s41598-022-24056-1

Warrington, E. K., and Shallice, T. I. M. (1980). Word-form dyslexia. *Brain* 103, 99–112.

Weiner, K. S., Sayres, R., Vinberg, J., and Grill-Spector, K. (2010). fMRI-adaptation and category selectivity in human ventral temporal cortex: regional differences across time scales. *J. Neurophysiol.* 103, 3349–3365. doi: 10.1152/jn.01108.2009

White, A. L., Kay, K. N., Tang, K. A., and Yeatman, J. D. (2023). Engaging in word recognition elicits highly specific modulations in visual cortex. *Curr. Biol.* 33, 1308–1320. doi: 10.1016/j.cub.2023.02.042

White, A. L., Palmer, J., Boynton, G. M., and Yeatman, J. D. (2019). Parallel spatial channels converge at a bottleneck in anterior word-selective cortex. *Proc. Natl. Acad. Sci. U. S. A.* 116, 10087–10096. doi: 10.1073/pnas.1822137116

Wimmer, H., and Ludersdorfer, P. (2018). "Searching for the orthographic lexicon in the visual word form area," in *Reading and Dyslexia: From Basic Functions to Higher Order Cognition*, eds T. Lachmann and T. Weis (Cham: Springer). doi: 10.1162/089892902317205285

Woodhead, Z. V. J., Barnes, G. R., Penny, W., Moran, R., Teki, S., Price, C. J., et al. (2014). Reading front to back: MEG evidence for early feedback effects during word recognition. *Cereb. Cortex* 24, 817–825. doi: 10.1093/cercor/bhs365

Woollams, A. M., Silani, G., Okada, K., Patterson, K., and Price, C. J. (2011). Word or word-like? Dissociating orthographic typicality from lexicality in the left occipito-temporal cortex. *J. Cogn. Neurosci.* 23, 992–1002.

Xu, J., Gannon, P. J., Emmorey, K., Smith, J. F., and Braun, A. R. (2009). Symbolic gestures and spoken language are processed by a common neural system. *Proc. Natl. Acad. Sci. U. S. A.* 106, 20664–20669. doi: 10.1073/pnas.0909197106

Xue, G., Chen, C., Jin, Z., and Dong, Q. (2006). Language experience shapes fusiform activation when processing a logographic artificial language: an fMRI training study. *Neuroimage* 31, 1315–1326. doi: 10.1016/j.neuroimage.2005.11.055

Yablonski, M., Karipidis, I. I., Kubota, E., and Yeatman, J. D. (2023). The transition from vision to language: distinct patterns of functional connectivity for sub-regions of the visual word form area. *bioRxiv* [Preprint]. doi: 10.1101/2023.04.18.537397

Yoncheva, Y. N., Zevin, J. D., Maurer, U., and McCandliss, B. D. (2010). Auditory selective attention to speech modulates activity in the visual word form area. *Cereb. Cortex* 20, 622–632. doi: 10.1093/cercor/bhp129

Zhao, L., Chen, C., Shao, L., Wang, Y., Xiao, X., Chen, C., et al. (2017). Orthographic and phonological representations in the fusiform cortex. *Cereb. Cortex* 27, 5197–5210.

Ziegler, J. C., and Muneaux, M. (2007). Orthographic facilitation and phonological inhibition in spoken word recognition: A developmental study. *Psychon. Bull. Rev.* 14:75. doi: 10.3758/bf03194031