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Abstract

Reading is both a visual and a linguistic task, and as such it relies on both general-purpose, visual mechanisms and more abstract, meaning-oriented processes. Disentangling the roles of these resources is of paramount importance in reading research. The present study capitalizes on the coupling of Fast Periodic Visual Stimulation (FPVS; Rossion, 2014) and MEG recordings to address this issue and investigate the role of different kinds of visual and linguistic units in the visual word identification system. We compared strings of pseudo-characters (BACS; C. Vidal & Chetail, 2017); strings of consonants (e.g,. *sfcl*); readable, but unattested strings (e.g., *amsi*); frequent, but non-meaningful chunks (e.g., *idge*); suffixes (e.g., *ment*); and words (e.g., *vibe*); and looked for discrimination responses with a particular focus on the ventral, occipito-temporal regions. The results revealed sensitivity to alphabetic, readable, familiar and lexical stimuli. Interestingly, there was no discrimination between suffixes and equally frequent, but meaningless endings, thus highlighting a lack of sensitivity to semantics. Taken together, the data suggest that the visual word identification system, at least in its early processing stages, is particularly tuned to form-based regularities, most likely reflecting its reliance on general-purpose, statistical learning mechanisms that are a core feature of the visual system as implemented in the ventral stream.

Keywords: Neural Entrainment, Reading, Linguistic Units, Visual Word Identification, Statistical Learning

Selective Neural Entrainment Reveals Hierarchical Tuning to Linguistic Regularities in Reading

1 In today's complex societies, printed words are among the most culturally

2 relevant visual objects processed by the human brain. Visual word recognition is

3 dexterously mastered by skilled readers, who can process written input as swiftly as

4 animals, plants or faces. However, printed words are not natural objects: reading and

5 writing constitute a relatively recent invention (Carr, 1999), making the literate brain a

6 case of an expert system shaped by cultural experience (Dehaene & Cohen, 2011) As

7 such, the neural underpinnings of reading have attracted much attention as a window

8 not only into the computational structure of the brain, but also into learning and

9 plasticity (e.g., Carreiras et al., 2014; Van Paridon et al., 2021).

10 Consistent evidence suggests the literate system relies on cortical resources

11 originally deputed to other functions (e.g., visual object processing) and reorganized (or

12 even recycled, Dehaene & Cohen, 2007) during literacy acquisition (as reviewed in, e.g.,

13 Dehaene et al., 2015). As a result, the neural underpinnings of reading would still

14 follow the principles that govern object recognition in the ventral stream (Dehaene

15 et al., 2005). A clear example comes from the hierarchical organization observed in the

16 macaque monkey, with an anterior-to-posterior progression of increasingly larger

17 receptor fields for more complex objects (Booth & Rolls, 1998; Riesenhuber & Poggio,

18 1999; Rolls, 2001). This structure might be ideally suited for language; many theories,

19 particularly of visual word identification, stipulate a hierarchy of progressively larger

20 processing units, from letters, to morphemes, to words (e.g., Crepaldi et al., 2010;

21 Grainger & Beyersmann, 2017; Grainger & Ziegler, 2011; Taft & Nguyen-Hoan, 2010).

22 Evidence for a graded selectivity for increasingly complex linguistic stimuli was

23 observed by Vinckier et al. (2007) in a portion of the ventral occipitotemporal cortex

24 (vOT), with the asymmetrical left profile that is generally associated with linguistic

25 processing (Cohen et al., 2002; Dejerine, 1892; Warrington & Shallice, 1980). Vinckier

26 et al. (2007) exposed skilled readers to a hierarchy of linguistic stimuli, ranging from

27 strings of pseudo-characters to real words, and including sequences of infrequent letters,

frequent letters but rare bigrams, and frequent bigrams but rare quadrigrams. BOLD-contrast responses indicated the presence of a hierarchical trajectory, with progressively selective responses for more complex stimuli. Moreover, this hierarchy unfolded in a posterior-to-anterior gradient, again in line with a fundamental organizational principle of the visual identification system more generally (e.g., DiCarlo et al., 2012).

In addition to unveiling the general organization of the orthographic system in the ventral stream, Vinckier et al. (2007)'s data raise several interesting questions. First, the hierarchy of stimuli that they used is entirely based on visual familiarity (i.e., frequency). Frequency of occurrence is a crucial element in the visual word identification system (e.g., Coltheart et al., 2001; Forster & Chambers, 1973; Norris, 2006). However, there are also units that, on top of frequency, have a peculiar linguistic status that would place them somewhat higher in this hierarchy (e.g., graphemes, such as *ch* in *chart*, or morphemes, such as *er* in *dealer*, might be more relevant for skilled readers compared to frequent, but linguistically unmarked units, e.g., *el* in *chapel*). Indeed, such higher linguistic constructs were repeatedly shown to have a crucial functional role in word identification (e.g., Amenta & Crepaldi, 2012; Grainger et al., 1991); what is then the relationship between said units, and the letter chunks considered in Vinckier et al. (2007)?

Second, Vinckier et al. (2007) found that real words did not differ from highly frequent, ortho-phonotactically legal quadrigrams (i.e., pseudowords). Albeit in line with previous evidence (Binder et al., 2006; Dehaene et al., 2005; Pammer et al., 2004; Price et al., 1996; Wydell et al., 2003), the lack of a reliable neural distinction between words and pseudowords has been object of a heated debate (as detailed in, e.g., Price, 2012; Taylor et al., 2013). Indiscriminate responses to real words (e.g., *rent*) and well-structured letter strings, previously unseen and meaningless (e.g., *tren*), suggest that visual word recognition might be entirely supported by abstract orthographic knowledge, consolidated by frequent encounters with regularly co-occurring patterns and beyond any lexical information. In line with this observation, some models of

visual word identification (Baayen et al., 2011; Binder et al., 2006; Xu & Taft, 2014) have entirely disposed of an orthographic lexicon – a functional and neural repository that stores word representations –, which has been at the core of neuropsychological models of reading in the 20th century (e.g., Morton, 1969; Patterson et al., 1987; Wernicke, 1874). These sublexical accounts have been challenged on the basis of studies showing selective lexical responses (Glezer et al., 2009; Kronbichler et al., 2007; Kronbichler et al., 2009), and proposing an interactive account of linguistic information, which would provide a source of top-down feedback for the early processing of orthographic input (e.g., Carreiras et al., 2014; Heilbron et al., 2020; Price & Devlin, 2003, 2011). In this breed of theories, both orthographic features and higher-order information (like phonology or semantics), as well as their mutual interaction, are at the core of the neural computations performed in the literate brain. A strict integration of information across the linguistic system has been also pushed by data showing early phonological and semantic effects upon the presentation of written words (e.g., Amenta et al., 2015; Chen et al., 2015; Rastle & Brysbaert, 2006; Sulpizio et al., 2022). Findings are still somewhat inconsistent on this topic, particularly on the neuroimaging side (e.g., Vignali et al. (2023) could not find reliable semantic effects until 320ms after stimulus onset, well after the emergence of orthographic effects). Overall, however, they certainly yield some credibility to the hypothesis that orthographic information might be strongly coupled with phonology and semantics, perhaps to the point that there is no, or very little temporal separation between. Overall, this ongoing debate clearly indicates that while we might have achieved rather refined knowledge of *where* the neural underpinnings of reading reside, we still have many important outstanding questions on *what* such areas code for (see Taylor et al., 2013, for the suggestion of an overarching framework).

A third important note concerns the distinction between semanticity and lexicality – carrying a meaning vs. being attested as a free-standing word. Naturally, the two aspects tend to coincide in the language; existing words (e.g., *salt*) differ from pseudowords (e.g., *falt*) *both* because words carry meaning *and* they are independent

chunks of letters that serve as functional units in the language. As a result, comparing words and nonwords does not allow to definitely adjudicate between the prevalence of semantic and lexical effects. Teasing the two apart, however, is absolutely critical for a theoretical understanding of reading, and may shed light on the specific function of the mid-fusiform gyrus (referred by many as the 'visual word form area', e.g., Dehaene & Cohen, 2011, a portion of the visual system whose involvement in linguistic processing has long been in the limelight of reading research). If cortical patches in these areas code for meaning, then specific linguistic functions are already performed at these early cortical stages. If, instead, this brain region is sensitive to lexicality, but not to semanticity per se, then the computations performed at this point of the visual hierarchy might be supporting linguistic and other, more general, visual material alike. That is, these areas might not feature language-specificity (e.g., Hillis et al., 2005; Wandell, 2011).

In the present work, we tackle these issues by taking advantage of a paradigm that recently became a prominent tool to address selective neural representations, namely Fast Periodic Visual Stimulation (FPVS, Rossion, 2014). By relying on frequency tagging, FPVS allows to isolate the brain's oscillatory response induced by the rapid, periodic presentation of visual items at a fixed rate (Norcia et al., 2015). The elicitation of such oscillatory responses has been recently combined with oddball designs: the regular embedding of items of a given kind (e.g., faces) in a stream of stimuli belonging to a different category (e.g., objects) creates a secondary, slower periodicity that is specific to the stimuli of interest, and that, crucially, can be only captured if the brain is indeed sensitive to the distinction (i.e., the two types of stimuli are supported by distinct neural representations). Critically, neural discrimination responses are elicited within few minutes of stimulation, are clearly quantifiable at the predefined frequency of interest, and yield high signal-to-noise ratios. Importantly, any response is gathered implicitly, in the absence of task-induced confounds, and is selective to the dimension that differentiates the two classes of items presented within the stimulation sequence.

115 This approach allowed Lochy et al. (2015) to obtain selective neural responses

116 for lexical items. Skilled readers were presented with periodic streams of stimuli (e.g.,

117 pseudowords, presented with a frequency of 10 Hz) in which word items appeared at

118 regular intervals (every 5 items, hence with a 2Hz frequency). Known words elicited a

119 neural entrainment, as evidenced by a sharp 2 Hz response measured at scalp,

120 reflecting the brain's ability to implicitly and rapidly discriminate lexical items in a

121 stream of readable, ortho-phonotactically legal, but non-existing pseudowords. A series

122 of studies adopting linguistic material (e.g., Lochy et al., 2018; Lochy et al., 2015;

123 Lochy et al., 2016) corroborated the role of FPVS as a powerful window into the neural

124 basis of visual word processing. Carefully controlled FPVS sequences could not only

125 address the existence of lexical representations, but also probe the specific

126 contributions of all the features that characterize linguistic information. Written input

127 is indeed composed of a series of nested levels, with phonological, orthographic and

128 semantic factors permeating different units of processing. In the eyes of a skilled

129 reader, known words are highly familiar, complex visual objects, which become

130 perceptually salient after a lifetime exposure (a mechanism akin to perceptual learning,

131 Fahle et al., 2002; Gilbert et al., 2001; Goldstone, 1998; Nazir et al., 2004; Nazir &

132 Huckauf, 2007). Structurally, visual words are combinations of known symbols (e.g.,

133 letters) that reflect the statistical co-occurrence regularities of the written language

134 (Araújo et al., 2015; Lin et al., 2011; Rudell & Hu, 2000). Words have also consistent

135 phonological (Aparicio et al., 2007; Braun et al., 2015; Dietz et al., 2005),

136 morphological (Leminen et al., 2016; Leminen et al., 2013; Leminen et al., 2019;

137 Vigliocco et al., 2006) and semantic associations (Devereux et al., 2013; Mirman &

138 Magnuson, 2009; Price et al., 2006).

139 The present study aimed at investigating the contribution of each of these

140 features by coupling MEG recordings with FPVS sequences, in a tightly controlled

141 hierarchy of contrasts. The use of MEG is an important novelty as compared to most

142 of the previous FPVS literature (but see, e.g., Pescuma et al., 2022); in fact, this

143 technique allows a reasonable spatial resolution, while maintaining the fine temporal

resolution that is required to study neural entrainment. By projecting the relevant FPVS response at source level, not only is possible to probe much more refined linguistic and visual representations, but also to appreciate their spatial arrangement in the ventral stream and, more generally, within the language processing network. Each contrast under study tackled a specific linguistic feature, seeking evidence for its relevance in skilled reading. Specifically, we assessed the presence of an Alphabetic response, by contrasting strings of consonants (e.g., *sfcl*) with sequences of items composed of artificial characters matching Roman letters on low-level visual features (BACS-2 characters, C. Vidal & Chetail, 2017). The same strings of consonants were then pitted against readable, but non-existing strings (e.g., *amsi*), to test the relevance of Readability. Readable items were subsequently compared to meaningless word endings that are highly frequent in the written language (e.g., *enso*), to investigate the impact of Familiarity. Such frequent units were then set against suffixes, which are frequent *and meaningful* sublexical items (e.g., *eria*), so that we could isolate sensitivity to meaning. The final comparison involved suffixes on one hand, and words (e.g., *idea*) on the other: a successful discrimination, here, would represent a purely lexical response, in that both classes of items are frequently attested in the written environment and consistently associated with meaning, and are exclusively differentiated on the basis of their lexical status.

Materials and Methods

Participants

Twenty-one volunteers (10 females; age: $M=27.2$, $SD=5.35$) took part in the experiment after giving written informed consent. All participants were right-handed native Italian speakers with normal or corrected-to-normal vision and no history of linguistic or neurological impairment. The experiment was conducted in accordance with the Declaration of Helsinki and was approved by the local ethical committee of the University of Trento (Prot. 2017-020).

Materials

Stimuli (illustrated in 1) comprised six categories of 32 items, all three-to-four

elements long (*M*=3.53, *SD*=0.507). Words (W, e.g., *idea*) were Italian nouns, and

Suffixes (Suff, e.g., *eria*, in English *ery*) were derivational morphemes. Frequent

Endings (HFE, e.g., *enso*, akin to the English *kle*) were highly frequent, meaningless

word endings attested in Italian. Pseudoendings (PE, e.g., *amsi*) were pronounceable

letter strings with a regular CV-structure (i.e., fourteen items: CCV, seventeen items:

VCCV, one item: VVV) that could potentially constitute ortho-phonotactically legal

word endings in Italian, but are not attested in the language. Nonword stimuli (NW,

e.g., *sfcl*) comprised random consonant strings and were thus unpronounceable. Finally,

Pseudofont (PF) strings were obtained by rendering random combinations of characters

from the BACS-2 serif artificial script (C. Vidal & Chetail, 2017), and resulted in

strings of symbols closely matching the visual characteristics of Latin characters (i.e.,

number of strokes, junctions, terminations, and serifs).

Among the linguistic items, Words, Suffixes and Frequent Endings had a high

and comparable written token frequency, measured by taking into account the cluster

position within the word (W: *M*=4.507, *SD*=0.580; Suff: *M*=4.983, *SD*=0.533; HFE:

M=4.229; *SD*=0.925), while Pseudoendings and Nonwords had a zero frequency, as per

their definition. Frequency metrics are computed on SUBTLEX-IT (Crepaldi et al.,

2013), which is based on a sample of 128 million words from movie subtitles (number of

types=517,564).

Given the strict constraints on the stimuli (e.g., the set of 32 suffixes we

employed here is very close to the complete set of 3- and 4-letter Italian suffixes), the

final selection includes some sub-optimal items. Specifically, seven suffixes were

homographic to words (e.g., *-ione*, with the Italian word for *ion*). We minimized the

potential impact of these items by fully randomizing the item order for each

participant; given the small number of the word-homographic suffixes, this drastically

reduced (eliminated, effectively) the possibility that they might yield extra frequencies

of resonance, or hamper the entrainment to the relevant frequencies by design.

Procedure

201   Stimuli were presented via sinusoidal contrast modulation at a frequency of 6 Hz

202 for 26.7 seconds, with each stimulus cycle lasting a total of 166.66 ms. Two types of

203 stimulation sequences were presented for each condition. In experimental trials, the

204 stimulation alternated between stimuli that belonged to two different categories (i.e.,

205 XYXYXY), such that stimuli from each category were presented every 333.33 ms (i.e.,

206 at a frequency rate of 6 Hz/2=3 Hz). In baseline trials, a sequence comprised stimuli

207 that belonged only to one category (i.e., xxxxxx). This design ensured that in each

208 experimental condition a differential signal (i.e., difference between alternating and

209 baseline sequences) at the stimulation frequency of 3 Hz reflected a neural response

210 that was selective to the property that distinguished the two categories of stimuli. It is

211 important to appreciate that this paradigm is intrinsically non-directional: a difference

212 between the experimental condition with suffixes and words and the baseline condition

213 with words only implies that the brain is sensitive to lexicality – not that it is

214 specifically sensitive to words *per se*, or to suffixes *per se*. Stated differently, the choice

215 of baseline (Word-Word, or Suffix-Suffix) does not affect the Word-Suffix condition. For

216 a schematic illustration of the experimental design and examples of stimulation

217 sequences, see Figure 1.

218   Five experimental conditions were used to isolate neural responses to stimuli

219 that are alphabetic (Nonwords vs. Pseudofonts; baseline: Nonwords), readable

220 (Pseudoendings vs. Nonwords; baseline: Pseudoendings), sublexical orthographic units

221 (Frequent Endings vs. Pseudoendings; baseline: Frequent Endings), sublexical

222 meaningful units (Suffixes vs. Frequent Endings; baseline: Suffixes), and lexical units

223 (Words vs. Suffixes; baseline: Words). There were 6 trials per experimental condition

224 and type of sequence, yielding a total stimulation time of 45 minutes: 26.7 s (trial

225 duration) X 5 experimental conditions X 2 types of sequences (alternating, baseline) X

226 6 trials. Trials consisted of unique sequences of 160 stimuli, each of which was

227 presented exactly five times in a pseudo-randomized fashion to avoid close repetitions;

228 additionally, the order of specific items was randomized for each participant, to avoid

²²⁹ potential list effects. The order of trial presentation was also pseudo-randomized to

²³⁰ avoid close repetitions of specific classes of items during the course of the experimental

²³¹ session. Trial presentations were separated by 15-second breaks.

²³²   Participants were seated at approximately 1 meter from a PROPixx DLP

²³³ projector (VPixx Technologies, Canada). The screen had a 1440x1080 pixels resolution

²³⁴ and a refresh rate of 120 Hz. Stimulus display was administered by PsychToolbox-3

²³⁵ (Brainard, 1997) on MATLAB R2015a (The MathWorks) in a Windows environment.

²³⁶ All stimuli were presented at the center of the screen. All alphabetic stimuli (i.e.,

²³⁷ Words, Suffixes, Frequent Endings, Pseudoendings and Nonwords) were presented in

²³⁸ lowercase characters, using the fixed-width Courier New font, whereas Pseudofonts were

²³⁹ presented in BACS-2 serif font. Both fonts were emboldened by 70% from their original

²⁴⁰ character weight to improve visibility. Each stimulus subtended horizontal and vertical

²⁴¹ visual angles of 2.58 and 0.64 degrees.

²⁴²   To ensure participants maintained a constant level of attention, they were

²⁴³ instructed to monitor the color change of a cross presented continuously at the center

²⁴⁴ of the screen. The change, from blue to red and vice versa, occurred three times in

²⁴⁵ each trial, independently of the experimental manipulation. Overall, participants'

²⁴⁶ performance in the color-change detection task was close to ceiling in accuracy

²⁴⁷ (M=97.8%, SD=14), and featured fast reaction times, (M=465 ms, SD=177).

²⁴⁸ Moreover, it was comparable across experimental trials (NW in PF=97%, SD=16,

²⁴⁹ reaction time: M=460 ms, SD=157; PE in NW=97.3%, SD=16, reaction time: M=469

²⁵⁰ ms, SD=188; HFE in PE=98.4%, SD=12, reaction time: M=468 ms, SD=175; Suff in

²⁵¹ HFE=97.8%, SD=14, reaction time: M=476 ms, SD=202; W in Suff=98.6%, SD=11,

²⁵² reaction time: M=452, SD=145) as well as baseline trials (NW in NW=97.3%, SD=16,

²⁵³ reaction time: M=466 ms, SD=189; PE in PE=98.1%, SD=13, reaction time: M=455

²⁵⁴ ms, SD=149; HFE in HFE=97.8%, SD=14, reaction time: M=477 ms, SD=216; Suff

²⁵⁵ in Suff=97.6%, SD=15, reaction time: M=461 ms, SD=160; W in W=98.4%, SD=12,

²⁵⁶ reaction time: M=462 ms, SD=173). A one-way ANOVA revealed no statistically

²⁵⁷ significant differences across conditions (accuracy: $F(9, 1230)$=0.522, p=0.859; reaction

258 time: $F(9, 1230)=0.894$, $p=0.53$).

MEG acquisition, Preprocessing and Frequency analysis

260 MEG data were recorded using a whole-head 306 sensor (204 planar

261 gradiometers; 102 magneto-meters) Vector-view system (Elekta Neuromag, Helsinki,

262 Finland). Participants' head position was continuously determined with respect to the

263 MEG helmet through five head position indicator coils (HPIs). MEG signals were

264 recorded at a sampling rate of 1000 Hz and online band-pass filtered between 0.1 and

265 300 Hz. At the beginning of each experimental session, fiducial points of the head (the

266 nasion and the left and right pre-auricular points) and a minimum of 300 other

267 head-shape samples were digitized using a Polhemus FASTRAK 3D 519 digitizer

268 (Fastrak Polhemus, Inc., Colchester, VA, USA). Raw data were processed through

269 MaxFilter 2.0 (Elekta Neuromag). For each participant, bad channels were identified

270 via visual inspection, and interpolated. Head displacements were inspected and

271 corrected through realignment to a single reference. After applying movement

272 compensation, external sources of noise were separated and removed by applying the

273 temporal extension of signal space separation (tSSS; Medvedovsky et al., 2009; Taulu

274 and Hari, 2009; Taulu and Simola, 2006).

275 Preprocessing and analysis were performed in MATLAB (MathWorks, Inc) with

276 a combination of Fieldtrip (Oostenveld et al., 2011), Brainstorm (Tadel et al., 2011)

277 and custom scripts. Continuous recordings from each participant were band-pass

278 filtered (0.1 - 100 Hz), downsampled (250 Hz) and epoched into 26.7-seconds trials,

279 which were realigned to the onset of the first stimulus (via a photodiode). Segments

280 contaminated by artifacts were identified through visual inspection and manually

281 removed (1.11%). To remove eye movements and heartbeat related artifacts from the

282 MEG signal we performed an Independent Component Analysis (ICA, Jutten &

283 Herault, 1991), separately for magnetometers and planar gradiometers. Eye movement

284 and pulse-related components were captured by correlating the independent component

285 (IC) time series with that of EOG and ECG channels.

286 For each participant, trials within each condition were averaged, and submitted

to a Fast Fourier Transformation. Given the length of the epochs, the frequency

resolution was $1/26.7=0.0374$ Hz. The spectra were then baseline-corrected by

subtracting from each frequency bin the mean of the surrounding 20 bins (10 from each

side, excluding local minima, maxima and immediately adjacent bins, as in e.g.,

Dzhelyova and Rossion, 2014); the response of interest was then defined as the

baseline-corrected amplitude at 3 Hz. A significant discrimination response, indexing

neural entrainments elicited by items belonging to different categories, was assessed by

comparing the 3Hz response in each experimental condition (e.g., Words in Suffixes)

with the corresponding baseline (i.e., Words in Words).

Sensor Space Analysis. Sensor level analyses were run at whole-brain level

through a non-parametric cluster permutation test (Maris & Oostenveld, 2007).

Differences at 3 Hz between the experimental and the baseline conditions were assessed

separately for magnetometers and combined planar gradiometers, by considering a

minimum neighborhood distance of 6 millimeters between sensors. Statistical

significance was assessed through a one-tail, dependent sample t-test with Monte-Carlo

estimates over 5000 permutations (significance level: $p<0.05$).

Source Space Analysis. Distributed minimum-norm source estimation (MNE,

Hämäläinen and Ilmoniemi, 1994) was applied following the standard procedure in

Brainstorm (Tadel et al., 2011). For twenty participants, anatomical T1-weighted MRI

images were acquired during a separate session in a Prisma 3T scanner (Siemens,

Erlangen, Germany) using a 3D MPRAGE sequence, 1-mm3 resolution, TR=2140 ms,

TI=900ms, TE=2.9ms, flip angle 12°, and segmented in Freesurfer (Fischl, 2012).

Co-registration of MEG sensor configuration and the reconstructed scalp surfaces was

based on around 300 scalp surface locations. As one participant did not undergo MRI

acquisition, we warped the default anatomy to match the shape defined by the digitized

points. Individual noise covariance matrices were computed from 1 s pre-stimulus

interval in all the available trials for each participant. The forward model was obtained

using the overlapping spheres method (Huang et al., 1999) as implemented in

Brainstorm. Fourier-transformed regression coefficients were then projected onto a

316 15000 vertices boundary element using a dynamic statistical parametric mapping

317 approach (dSPM; Dale et al., 2000), assuming dipole sources to be perpendicular to the

318 cortical surface. Individual results were spatially smoothed (3mm FWHM) and

319 projected to a default template (ICBM152).

320   Differences at 3 Hz between experimental and baseline conditions were then

321 assessed at source level in the vertices of predefined regions of interest, obtained from

322 the Desikan-Killiany cortical atlas (Desikan et al., 2006). The ROIs selected for the

323 source-level analysis corresponded to some of the most prominent cortices involved in

324 reading, such as fusiform (e.g., Dehaene et al., 2002), lingual (e.g., Raschle et al., 2011),

325 inferior parietal (e.g., Sliwinska et al., 2015), inferior temporal (e.g., Dien et al., 2013),

326 lateral occipital (e.g., Borowsky et al., 2007) and middle temporal (e.g., Turkeltaub

327 et al., 2003). On each ROI, significant responses were assessed via nonparametric

328 cluster permutation test (N=5000, $p<0.05$; Maris & Oostenveld, 2007). Non-significant

329 effects were here explored through JZS Bayes Factor analysis (BF_{10}, scale factor

330 $r=0.707$; Rouder et al., 2009), which provides quantifiable evidence in support of H1 or

331 H0, thus allowing to support the null hypothesis itself (Leppink et al., 2017).

Results

333   **Sensor Space.** The profile of the neural responses gauged at the frequencies of

334 interest (3 and 6 Hz) for both experimental and control trials is depicted in Figure 2.

335   As shown in Figure 3, a clear discrimination response indicated sensitivity to the

336 alphabetic nature of the items (NW-PF vs. NW-NW), emerging in a diffused area for

337 both planar gradiometers ($t_{(20)}=311.13$, $p=0.0002$, $g=0.83$ [0.53, 1.13]) and

338 magnetometers ($t_{(20)}=274.17$, $p=0.0002$, $g=0.81$ [0.49, 1.12]). Lexical items embedded

339 in suffixes (W-Suff vs. W-W) also elicited a marked discrimination response, with

340 left-lateralized topography for both planar gradiometers ($t_{(20)}=80.30$, $p=0.0004$, $g=0.65$

341 [0.12, 1.16]) and magnetometers ($t_{(20)}=74.28$, $p=0.0002$, $g=0.71$ [0.18, 1.22]).

342   No discrimination response emerged as statistically significant for the other

343 contrasts. Readability (PE-NW vs. PE-PE) resulted in a cluster that did not reach

344 significance in planar gradiometers ($t_{(20)}=9.39$, $p=0.13$, $g=0.61$ [-0.91, 2.01]) and no

345 cluster for magnetometers. Familiarity (HFE-PE vs. HFE-HFE) produced a

346 non-significant cluster for magnetometers ($t_{(20)}$=8.81, p=0.233, g=1.03) and no cluster

347 for gradiometers. No significant cluster emerged for meaningful sublexical units

348 (Suff-HFE vs. Suff-Suff).

349 **Source Space.** Significant discrimination responses in the predefined ROIs are

350 displayed in Figure 4. At source level, a 3Hz discrimination response for the alphabetic

351 nature of the stimuli (NW-PF vs. NW-NW) emerged bilaterally in all the areas of

352 interest (as summarized in Table 1).

353 A discrimination between readable stimuli and strings of consonants (PE-NW

354 vs. PE-PE) yielded a right-lateralized profile, involving fusiform ($t_{(20)}$=161.31,

355 p=0.0216, g=1.23 [0.82, 1.63]), inferotemporal ($t_{(20)}$=134.31, p=0.0206, g=1.30 [0.86,

356 1.72]), lateral occipital ($t_{(20)}$=204.39, p=0.024, g=1.16 [0.82, 1.49]) and middle

357 temporal cortices ($t_{(20)}$=105.35, p=0.0332, g=0.92 [0.48, 1.34]).

358 Familiarity (HFE-PE vs. HFE-HFE) elicited significant responses only in the

359 right inferior temporal area ($t_{(20)}$=220.03, p=0.0178, g=1.14 [0.81, 1.47]).

360 Consistently with the results observed in sensor space, suffixes embedded in

361 frequent endings yielded no significant response in the predefined ROIs. This null result

362 was further explored through a JZS Bayes Factor analysis across ROIs, which, where

363 conclusive, provided moderate evidence in favor of the null hypothesis (as described in

364 Table 2).

365 Differences between words and suffixes (W-Suff vs. W-W) were traced in

366 bilateral fusiform (left: $t_{(20)}$=227.12, p=0.0174, g=1.11 [0.77, 1.44]; right: :

367 $t_{(20)}$=283.35, p=0.004, g=0.94 [0.65, 1.22]), together with two significant clusters in left

368 inferior temporal (first: $t_{(20)}$=230.97, p=0.0206, g=1.01 [0.68, 1.33]; second:

369 $t_{(20)}$=186.03, p=0.029, g=0.93 [0.55, 1.29]), left lateral occipital ($t_{(20)}$=580.00,

370 p=0.0008, g=0.77 [0.57, 0.97]) and left lingual ($t_{(20)}$=436.91, p=0.004, g=1.23 [0.98,

371 1.48]).

General Discussion

372   The present study investigated the neural underpinnings of visual word

373   identification, by asking which linguistic features might be rapidly and automatically

374   discriminated by the reading brain. With this aim, we paired MEG recordings with

375   Fast Periodic Visual Stimulation sequences (FPVS, Rossion, 2014) constructed

376   specifically to isolate some of the fundamental features of written text, in a carefully

377   controlled hierarchy of nested contrasts. In this design, observing neural entertainment

378   at the frequency with which classes of items were presented implicitly indexes a

379   selective discrimination for the feature that differentiates the two groups of items.

380   Interleaving words (e.g., *idea*) and suffixes (e.g., *eria*) revealed a strong Lexicality

381   response, already detectable at sensor level. Similarly, the alternation of

382   pseudo-characters and letter strings (e.g., *sfcl*) revealed a strong sensitivity to the

383   alphabetic nature of the stimuli, also observable at both sensor and source levels. More

384   subtle contrasts, addressing the role of Readability (with strings of consonants, e.g., *sfcl*

385   vs. pseudoendings, e.g., *ampi*) and Familiarity of letter strings (with high frequency

386   endings, e.g., *enso* vs. pseudoendings, e.g., *ampi*), were captured only at source level.

387   Notably, our results did not reveal a Meaningfulness response, as assessed by

388   contrasting suffixes (e.g., *eria*) with equally frequent, but meaningless word endings

389   (i.e., *enso*).

390   One way to interpret these findings is that the reading system is automatically

391   responsive to lexicality. Such a response is characterized by a predominantly

392   left-lateralized profile, arising in areas typically associated with word identification and

393   processing, such as left lateral occipital, lingual and inferotemporal cortices (Binder &

394   Price, 2001; Borowsky et al., 2007), as well as the bilateral fusiform gyrus (Cohen

395   et al., 2002; Dehaene et al., 2002; Fiez & Petersen, 1998; Puce et al., 1996). This

396   selective neural discrimination for lexicality lends some support to the existence of an

397   orthographic lexicon, consistently with more recent neural models of reading (Taylor

398   et al., 2013). Nevertheless, the spatial resolution of non-invasive human neuroimaging

399   in general, and of MEG in particular, requires a word of caution in interpreting these

results, especially at a cognitive level. Specifically, our findings cannot pinpoint whether this Lexical response originates from a set of individual neurons specifically selective to words per se, or rather from a coordinated, large ensemble of neurons with a less granular preference. Therefore, the present study cannot arbitrate between localist and distributed accounts of lexical neural codes at a mechanistic level (Bowers, 2009, 2017; Quian Quiroga & Kreiman, 2010; Roy, 2012; Vankov & Bowers, 2017).

Neuroimaging evidence has been fairly elusive as to whether the reading brain responds specifically to existing words (as opposed to well formed strings of letters, e.g., Binder et al., 2006; Dehaene et al., 2005; Pammer et al., 2004; Price et al., 1996; Wydell et al., 2003). The adoption of neural adaptation techniques has provided a decisive methodological boost in this direction, by allowing the tapping into selective neuronal tunings to stimulus features (Grill-Spector et al., 2006; Norcia et al., 2015). Importantly however, while previous studies succeeded in capturing selective adaptation to lexical forms (e.g., Glezer et al., 2009; Lochy et al., 2015), they generally did so by pitting words against pseudowords, thus adopting two classes of items that differ in more than one relevant dimension. Written words are indeed meaningful linguistic objects, with a known phonological and orthographic form, while well-structured pseudowords are, albeit pronounceable (Taylor et al., 2013), unknown strings of letters. Contrariwise, the Lexical response obtained in the present study stems from an unprecedentedly tight comparison, realized by contrasting fully-fledged, real words with suffixes. Morphemes like *-ness* or *-er* are attested in the language with high frequency, and due to their derivational properties, they alter the meaning of stems they are combined with in a highly predictable and consistent manner (e.g., kind*ness*, high*ness*, sing*er*, danc*er*) – thus, they have a specific meaning (Bloomfield, 1933; Bybee, 1988). Naturally, the nature of this meaning is often different from words; for example, suffixes might be seen as carrying functional information, which modifies the core lexical message carried by the stem (e.g., *X-ness* as the state of being X; Marelli & Baroni, 2015)[1]. Similar to words, however, suffixes forge strong and

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[1]Note, however, this does not have implications of strength, or relative importance; for example,

consistent associations between their orthographic form and a semantic concept (e.g.,

the suffix *-er* conveys agency), and they mostly differ from words in their sublexical,

rather than lexical, status, in that they cannot appear in isolation as independent

linguistic units. Therefore, the adoption of morphemes allows to uniquely overcome the

rather coarse characterization of the lexical discrimination obtained with pseudowords,

and supports the presence of a neural response that is specifically lexical, not related to

meaning, frequency of occurrence or readability alone.

Indubitably, sublexical morphemes such as suffixes play a fundamental function

in visual word identification. Behavioral evidence has extensively supported the role of

morphemes in the recognition of complex words (e.g., Amenta & Crepaldi, 2012;

Bonandrini et al., 2023; Giraudo & Voga, 2014; Rastle & Davis, 2008), including

experiments where, similar to the present study, suffixes where presented in isolation

and under tight visual conditions (masked priming; e.g., Andoni Dunabeitia et al.,

2008). This was further corroborated by several neuroimaging studies (e.g.,

Beyersmann et al., 2021; Davis et al., 2004; Devlin et al., 2004; Gold and Rastle, 2007;

Lavric et al., 2012; Lehtonen et al., 2011; Lewis et al., 2011; Pescuma et al., 2022; for a

recent review, see Leminen et al., 2019). Nevertheless, the vast majority of the

available studies investigated the role of morphemes by embedding them in a lexical

context (i.e., morphologically complex words, e.g., *kind-ness*, or pseudowords, e.g.,

table-ness), and thus leaves their specific neural characterization somewhat

underspecified. The present study provides novel insight by indicating that, when

presented in isolation, suffixes are not reliably distinguished from frequent word

endings. Such a finding nicely reckons with recent experimental evidence obtained in

artificial lexicon studies showing that skilled readers can carve affix-like units on the

sole basis of their frequency of occurrence, and even in the absence of phonological or

semantic information (e.g., Chetail, 2017; Lelonkiewicz et al., 2020, 2023). Collectively,

this body of evidence does not abide by cognitive models of morphological processing

that assume dedicated representations for meaningful, sublexical units (e.g., Crepaldi

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suffixes are generally assumed to be the morphological head of derived words.

et al., 2010; Taft, 2004; Taft & Nguyen-Hoan, 2010), and is better aligned with

accounts emphasizing perceptual and orthographic mechanisms for the decomposition

of complex words (e.g., Grainger & Beyersmann, 2017). Particularly, Grainger and

Beyersmann (2017) theorize that while the recognition of sublexical units is achieved on

the basis of orthographic factors, their semantic activation is primarily driven by the

lexical context in which they appear (e.g., the meaning of *-er* would be activated when

the suffix is presented in an adequate context, like *sing-er*). Coherently, and in spite of

their morphological status, isolated suffixes would be no more perceptually salient than

other highly frequent word endings.

Taken together, our results seem to reflect the sensitivity of the reading system

to form-based regularities, by tapping into the bottom-up processing of visuo-linguistic

material. Words stood out as independent units even if compared with another set of

meaning-bearing items, consistently with theories of perceptual learning (Fahle et al.,

2002; Gilbert et al., 2001; Goldstone, 1998). The lexical knowledge available to skilled

readers is indeed not only reliant on linguistic information, but also on the visual

familiarity that results from an extensive experience with written text, where frequent

and repeated encounters with printed words would consolidate their representation as

complex but unitary shapes, rather than combination of features (Gilbert et al., 2001;

Kennedy et al., 2000; Nazir & Huckauf, 2007). Consequently, individual words would

become privileged units of processing that "pop-out" (Nazir et al., 2004) to the eyes of

a skilled reader, particularly if displayed in their most prototypical form (as, for

instance, in a horizontal orientation, Nazir & Huckauf, 2007; Wimmer et al., 2016).

Critically, word tokens are generally surrounded by empty spaces, which provide

privileged anchor points to infer letter information and, subsequently, word identity

(Fischer-Baum et al., 2011; Grainger & Beyersmann, 2017; Jacobs et al., 2013). Such

perceptual salience might not be comparably bestowed upon suffixes, which, although

frequent and meaningful, are bound to appear within complex words and are never

encountered independently. Coherently, bound morphemes like suffixes were not

significantly discriminated from highly frequent, but meaningless word endings; both

classes of items are comparably familiar in their form arguably and are equally

supported by the perceptual experience of skilled readers. These considerations raise an

interesting point about the contribution of more linguistic and more perceptual factors

to our reading experience – and, more importantly, how they shape the cognitive and

neural architecture underlying reading. Of course, lexicality is a very rich linguistic

construct, which has important ramifications in virtually all aspects of our linguistic

experience (e.g., phonology, syntax). Yet, we always see words surrounded by blanks,

so it is not so unlikely that this becomes a fundamental piece of information that our

lexical system captures. We conceive these perceptual and linguistic factors as integral

parts of our visual word identification system; as allied, not competitors, in determining

the way in which the brain processes letters and words. Certainly, the present study

cannot really tease these perceptual and linguistic factors apart; this was not the goal

of the present work. Future studies, perhaps capitalizing upon orthographic systems

that do not build upon inter-word spacing (e.g., Mandarin Chinese), might shed some

light on the respective contributions of visual (e.g., boundedness) and linguistic (i.e.,

meaning) factors in reading.

Additionally, the role of context in morpheme processing extends beyond

perceptual factors, as attested for instance by studies focusing on inflectional affixes.

Word and phrase contexts are critical for affix interpretation in languages with rich

inflectional systems (Franzon & Zanini, 2023; Pescuma et al., 2021), as well as for

disambiguating homographs (Franzon et al., 2021; Franzon & Zanini, 2023). Moreover,

the presence of semantic content in inflectional morphemes can even extend as far as to

affect word processing and recognition (Arcara et al., 2019; Zanini et al., 2020),

suggesting that the presence of a minimal context plays a fundamental role in allowing

readers to access the meaning of sublexical units.

Admittedly, this might depend, at least in part, on the specific paradigm

adopted. FPVS enhances the visual, fast, automatic and implicit processing of letters

and strings; therefore, it certainly taps into what can be thought as the perceptual

front-end of the reading system. This might reconcile the highly relevant role that

515 morphemes play in visual word identification (e.g., Amenta & Crepaldi, 2012;

516 Bonandrini et al., 2023) with the lack of a suffix-specific response observed in the

517 present work. Nevertheless, the present data indicates that words and suffixes have

518 different statuses in the visual word identification system, a conclusion that speaks

519 against what many cognitive models postulate (e.g., Crepaldi et al., 2010; Grainger &

520 Ziegler, 2011; Taft & Nguyen-Hoan, 2010).

521   With respect to the lack of semantic effects, it is interesting to note that some

522 FPVS study was able to elicit meaning-based responses (Stothart et al., 2017).

523 However, these effects emerged with images, not words, and using slower oddball

524 cycles; these methodological differences might be critical for tackling higher-level

525 processing. There is also neuroimaging evidence suggesting very early semantic

526 activation for written words (e.g., Chen et al., 2015; Sulpizio et al., 2022). However,

527 this literature did not use FPVS, and the specific timing of meaning activation in the

528 brain after the presentation of written words is still quite inconsistent across studies

529 (e.g., Vignali et al., 2023).

530   The selective neural responses for Alphabetic stimuli, as well as for Readability

531 and Familiarity, also sit well with a bottom-up account of the present results. Strings

532 of consonants embedded in pseudo-characters elicited a strong and diffused response,

533 involving all the predefined regions of interest considered. Such a pervasive Alphabetic

534 response suggests that, despite pseudo-characters being carefully matched onto letters'

535 low-level visual features (C. Vidal & Chetail, 2017), letter-based configurations were

536 markedly more familiar to skilled readers (Lochy et al., 2018; Lochy et al., 2015; Lochy

537 et al., 2016; Thesen et al., 2012; van de Walle de Ghelcke et al., 2020; Vinckier et al.,

538 2007; Wang et al., 2021). When contrasted with strings of consonants, readable but

539 non-attested sequences of letters (e.g., *ampi*) elicited a right-lateralized response

540 encompassing fusiform, lateral occipital and both middle and inferior temporal ROIs,

541 areas reportedly involved in vowel processing, as opposed to consonants (Carreiras &

542 Price, 2008; Carreiras et al., 2009) and non-speech (Obleser et al., 2006; Uppenkamp

543 et al., 2006). Critically, ortho-phonotactically legal items are not only readable, but

also more word-like (as opposed to consonant strings), a feature considered to be at the

core of the neural underpinnings of reading (e.g., Binder et al., 2006; Vinckier et al.,

2007), and consistent with a form-based regularity account of the present findings. In a

transparent orthography like Italian, orthographic units are unambiguously associated

with a phonological pattern, thus hampering a clear-cut distinction between the effects

of familiarity and readability *per se*. Nevertheless, recent neuroimaging evidence

obtained in Hebrew (Weiss et al., 2015) appears to support a privileged role for

familiarity over orthographic transparency. By exposing skilled readers to words with

vowel sounds rendered either through vowels alone, or with the adoption of diacritic

markers, Weiss et al. (2015) observed that the more familiar format (i.e., without

diacritics) provided a major processing advantage. This advantage overrode the

increased transparency ensured by the presence of diacritics, hence pinpointing visual

familiarity as a key feature in the neural processing of readable stimuli (see, e.g.,

Chetail & Boursain, 2019; Kinoshita et al., 2021; Marcet et al., 2020; Perea et al., 2020;

Perea et al., 2022, for recent behavioral investigations on the topic). Critically, Italian

has a much more transparent orthography than Hebrew, and this might affect readers

in their propensity to rely on visual familiarity; further studies relying on direct

cross-linguistic comparisons are required to better describe the roles of familiarity and

orthographic depth in reading performance.

Finally, the contrast between readable but non-existing word endings (e.g.,

ampi) and highly frequent word endings (e.g., *enso*) resulted in a selective neural

entrainment sourced in an anterior portion of the right inferotemporal ROI. Behavioral

research on reading pullulates with effects of written frequency, which have been often

considered proxies of learned representations (Baayen et al., 2007; Burani and

Thornton, 2003; Colé et al., 1989; Monsell et al., 1989; Preston, 1935; Taft, 1979, 2004;

see, e.g., Brysbaert et al., 2018; Ellis, 2002 for reviews). Neuroimaging studies indicate

that frequency effects can be traced throughout several visual word identification

processes (Barber & Kutas, 2007), and that frequency-modulated activations might be

housed in occipitotemporal regions (e.g., Frost et al., 2005; Keller et al., 2001; Kuo

et al., 2003; Montani et al., 2019; Vinckier et al., 2007; but see, e.g., Fiebach et al., 2002; Fiez et al., 1999; Ischebeck et al., 2004 for diverging patterns of results). Notably, written frequency effects are reminiscent of a more general recognition mechanism of extraction and storage of recurring patterns, including words, faces and other salient visual objects (Kronbichler et al., 2004; Y. Vidal et al., 2021). In keeping with this conjecture, the selective neural entrainment elicited by high-frequency clusters in the present study stems from a portion of the inferior temporal cortex, which constitutes a cornerstone of visual object encoding (DiCarlo et al., 2012). Particularly, this area has been attested to support the processing of orthographic items in primates (Rajalingham et al., 2020), and qualifies as a powerful visual processing resource to be recycled (Dehaene & Cohen, 2007) by the more phylogenetically recent reading system.

The absence of a discrimination response for meaningfulness (i.e., between high-frequency endings and suffixes) and the presence of effects that predominantly relate to visual familiarity (e.g., frequent word endings vs. unattested letter strings) seem to suggest that the present data are mostly driven by bottom-up processes. This conclusion is also supported by a series of methodological considerations. The FPVS technique allows to detect automatic and implicit neural discrimination responses within a few minutes of stimulation, by capitalizing on a rapid presentation rate and absence of explicit engagement with the experimental material (Liu-Shuang et al., 2014; Norcia et al., 2015; Rossion, 2014). Critically, stimuli are presented via sinusoidal contrast modulation (from white background to full contrast and back) with a frequency of 6 Hz, thus each item remains on screen for about 167 ms, reaching full contrast at 83 seconds, and with an actual visibility duration of around 140 ms (considering that stimuli can be recognized at low contrast levels, such as 20%, Lochy et al., 2015; Lochy et al., 2016). Such a brief presentation is complemented with the perceptual masking induced by sequential stimulus presentation, which unfolds without any inter-stimulus interval (in line with RSVP paradigms; see Retter et al., 2018, for a related discussion). As a result, the present FPVS design is likely to tap into rather early stages of processing, which are probably informed more by bottom-up, visual and

602 orthographic information rather than by top-down, higher level information (such as

603 semantics).

604 Remarkably, the demanding nature of the stimulation stream is also consistent

605 with the spatial profile of the more subtle responses obtained along the hierarchy of

606 contrasts. Indeed, while linguistic processes are generally associated with activity in the

607 left hemisphere (Dehaene et al., 2001; Pinel & Dehaene, 2010), the right hemisphere is

608 reportedly more resilient to fast and degraded visual presentations of alphanumeric

609 stimuli (e.g., Asanowicz et al., 2017; Hellige & Michimata, 1989; Jonsson & Hellige,

610 1986; Michimata & Hellige, 1987; Sergent & Hellige, 1986; Verleger et al., 2013;

611 Verleger et al., 2011). Coherently, while a selective Lexical response resulted in a

612 prototypical left-lateralized profile, more subtle, sublexical units could enjoy weaker

613 support from pre-existent linguistic representations, which allowed the right-lateralized,

614 perceptual response to be more easily captured. Future research is needed to address

615 the impact of different experimental parameters, by systematically tuning the

616 stimulation frequency to the feature of interest, and assessing whether different

617 presentation rates could further qualify the neural entrainment hereby observed (for a

618 related discussion, see Alonso-Prieto et al., 2013; Rossion, 2014).

619 Overall, the present results contribute to our understanding of the general

620 architecture of the visual word identification system, and contribute to addressing some

621 critical open issues, such as the relationship between letter statistics and linguistic

622 units, as well as the role of lexicality and its relationship with meaning. When

623 semantics are decoupled from existence as an independent lexical unit – that is, from

624 being a recurrent string of letters flanked by blanks – the cognitive system does not

625 show much sensitivity to the former, and quite a lot for the latter (at least as far as

626 assessed in a FPVS setting). One hypothesis we can advance in this regard is that

627 FPVS might reduce the importance of the usual feedback signal that the fusiform gyrus

628 receives from higher-level language circuitry (Ben-Shachar et al., 2007; Devlin et al.,

629 2006; Wandell, 2011), boosting visual effects and hampering the semantic factors. In

630 such case, the widespread lexicality effect observed could be interpreted as mostly

reliant on the bottom-up process of perceiving a unitary visual object: the word. The FPVS lexicality signal attested here extends well beyond the posterior fusiform, and includes the right anterior fusiform gyrus, the lateral occipital gyrus and the inferior temporal gyrus on the left. These data would then suggest that the sensitivity of visual string processing to chunks of letters that co-occur with specific statistical patterns climbs up the visual identification system much more than what might have been previously thought. Not only the posterior fusiform would be more about letter co-occurrence statistics than meaning and 'proper' linguistic content (e.g., Dehaene & Cohen, 2011; Hillis & Caramazza, 1991; Nobre et al., 1994), but the statistics and, more generally, the more perceptual aspects of visual word identification would play a relevant role upstream. This would be in line with data (e.g., Y. Vidal et al., 2021) and theories (e.g., Dehaene & Cohen, 2007) suggesting that the computational structure of the visual word identification system might be strongly determined by the pre-existing, biologically-constrained processing mechanisms that reside in these areas.

In conclusion, the present study capitalized on FPVS and MEG recordings to shed some new light on which linguistic features underpin reading. Implicit discrimination responses emerged in a tightly controlled hierarchy of contrasts, whose extremes revealed a strong sensitivity to letters and lexical items. Sensitivity to the intermediate layers – the mere association with meaning, familiarity and readability – was generally weaker, if present at all. Taken together, these results provide novel insight into the brain's sensitivity to form-based regularities, and highlight the relevance of perceptual familiarity at the early stages of visual word identification.

Declarations

Code and Data Availability Statement

Data and materials for the experiment reported in this study are available at

https://osf.io/u58w7/.

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ROI	t value	Effect size g	$\Pr(>|t|)$	
Left Fusiform	1059.21	1.57 [1.36, 1.77]	<0.001	***
Right Fusiform	956.08	1.91 [1.69, 2.12]	<0.001	***
Left Inferiorparietal	1060.81	1.35 [1.18, 1.52]	<0.001	***
Right Inferiorparietal	1315.81	1.37 [1.22, 1.52]	<0.001	***
Left Inferotemporal	903.83	1.29 [1.10, 1.48]	<0.001	***
Right Inferotemporal	1052.57	1.57 [1.38, 1.75]	<0.001	***
Left Lateral Occipital	1609.02	1.48 [1.32, 1.65]	<0.001	***
Right Lateral Occipital	1313.58	1.62 [1.45, 1.79]	<0.001	***
Left Lingual	921.25	1.59 [1.37, 1.80]	<0.001	***
Right Lingual	729.36	1.70 [1.47, 1.92]	<0.001	***
Left Middle temporal	603.84	1.03 [0.82, 1.25]	<0.001	***
Right Middle temporal	1141.24	1.38 [1.20, 1.55]	<0.001	***

Table 1

Alphabetic Response (PF-NW vs. NW-NW), Source Level Results

ROI	Number of Vertices	$BF_{10}<1/3$	$BF_{10}>3$
Left Fusiform	268	156 (58%)	0
Right Fusiform	255	186 (72%)	0
Left Inferiorparietal	351	70 (19%)	39 (11%)
Right Inferiorparietal	421	219 (52%)	20 (5%)
Left Inferotemporal	307	155 (50%)	0
Right Inferotemporal	316	213 (67%)	9 (3%)
Left Lateral Occipital	371	207 (55%)	4 (1%)
Right Lateral Occipital	367	251 (68%)	0
Left Lingual	246	154 (62%)	0
Right Lingual	227	186 (82%)	0
Left Middle temporal	277	191 (69%)	9 (3%)
Right Middle temporal	324	205 (63%)	19 (6%)

Table 2

Suff-HFE vs. Suff-Suff contrast, Source Level Bayes Factor Analysis. For each ROI, the table reports the total number of vertices, the ones providing moderate evidence in favor of the Null hypothesis (i.e., with $BF_{10}<1/3$) and those moderately supporting the alternative (i.e., with $BF_{10}>3$).
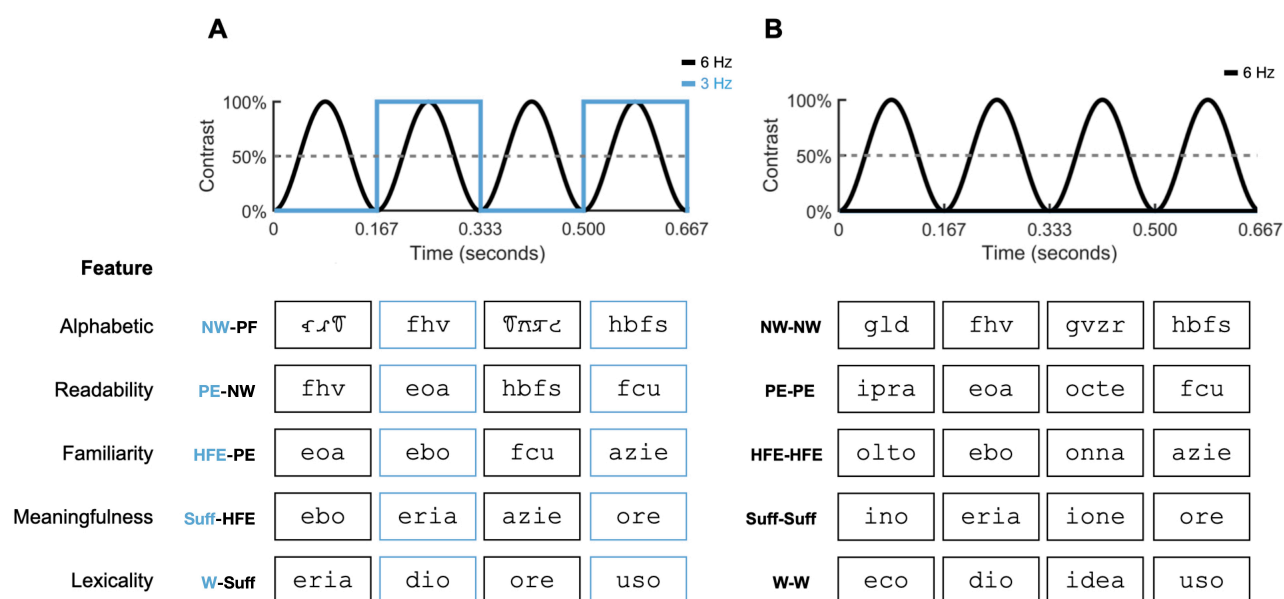
Figure 1

Experimental Paradigm. All stimuli were presented by sinusoidal contrast modulation; the figure displays four cycles of 166.66 ms. In the experimental trials (panel A) stimuli from two classes were alternated, to isolate neural responses selective to discriminative properties (e.g., letter strings and pseudo-characters differ solely on the basis of their alphabetic nature). Examples are given for the five different properties of interest: alphabetic (Nonwords, NW, vs. Pseudofonts, PF), readability (Pseudoendings, PE, vs. Nonwords, NW), familiarity (High frequency endings, HFE, vs. Pseudoendings, PE), meaningfulness (High frequency endings, HFE, vs. Suffixes, Suff), and lexicality (Words, W, vs. Suffixes, Suff). The control trials (panel B) comprised items belonging to the same category (e.g., a single stream of letter strings), and served as a baseline condition for the discriminative nature of the neural responses yielded by the experimental trials. Particularly, the difference between the 3Hz response in experimental and baseline trials would represent a genuine discrimination between items belonging to two different experimental categories, thus reflecting the feature under study.
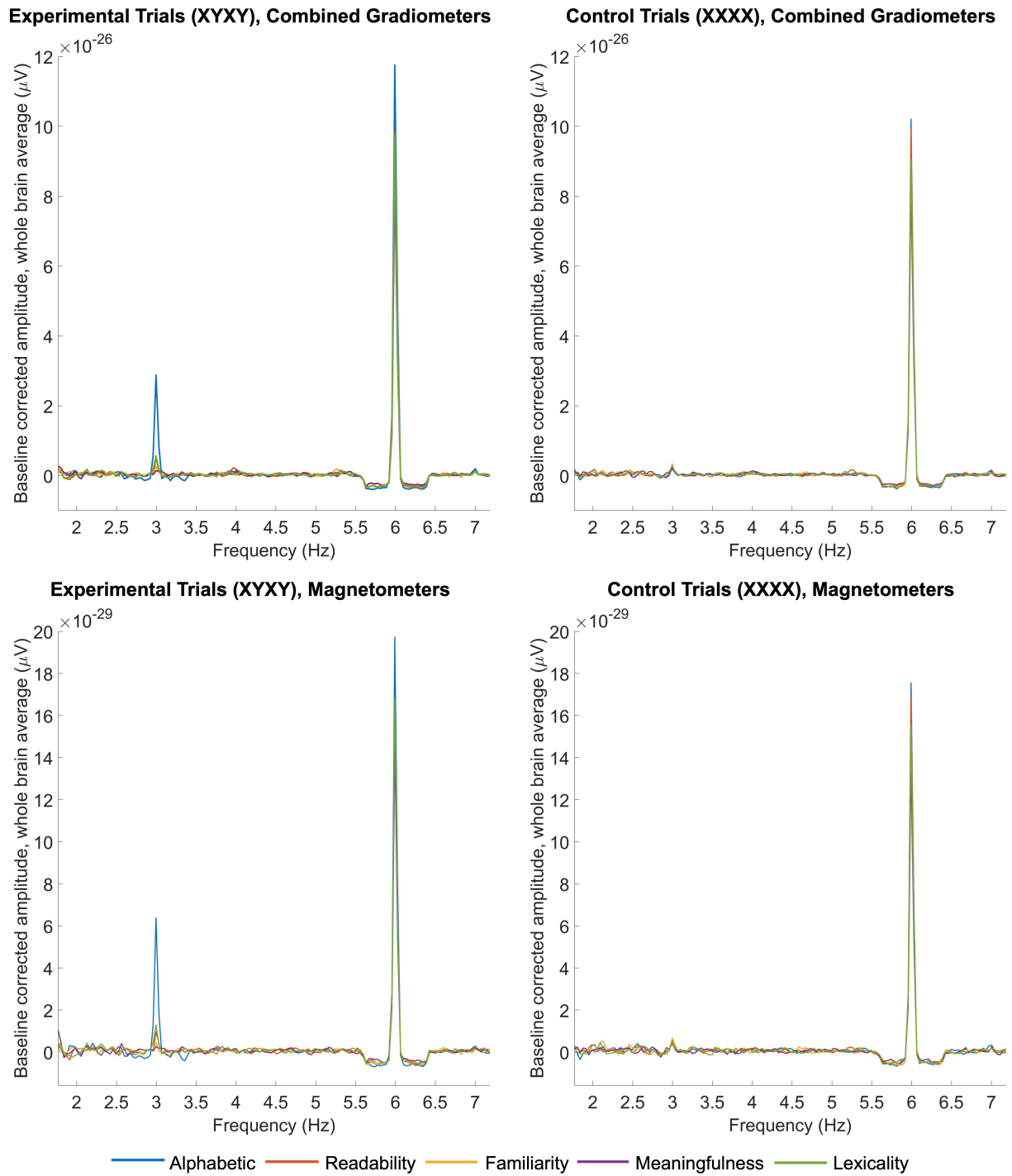
Figure 2

Grand-averaged, whole-brain baseline-corrected amplitude (V) spectra for the different conditions across sensor types. Critically, the profiles indicate that the response is confined to the frequencies of interest (3 and 6 Hz).
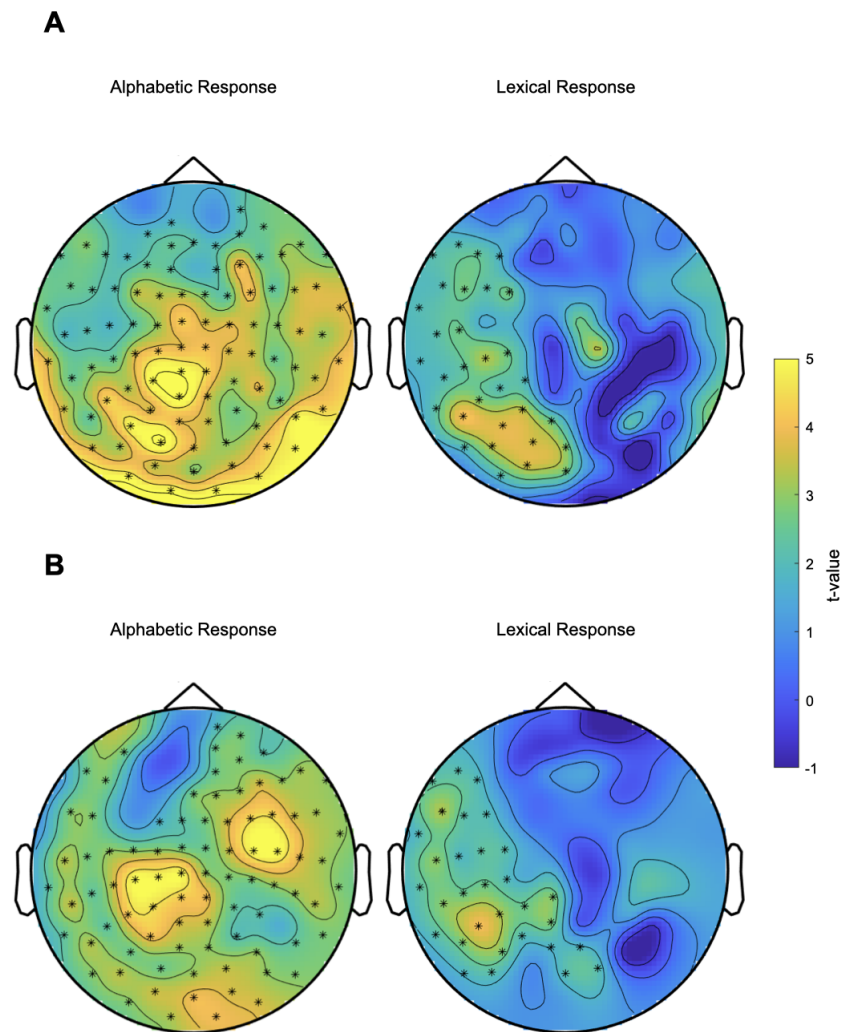
Figure 3

Sensor level results. One significant, largely diffused cluster indicated the discrimination of alphabetic stimuli, while a left-lateralized significant cluster was associated with lexical discrimination. The topography of the effects is comparable across planar gradiometers (panel A) and magnetometers (panel B) for both discrimination responses.
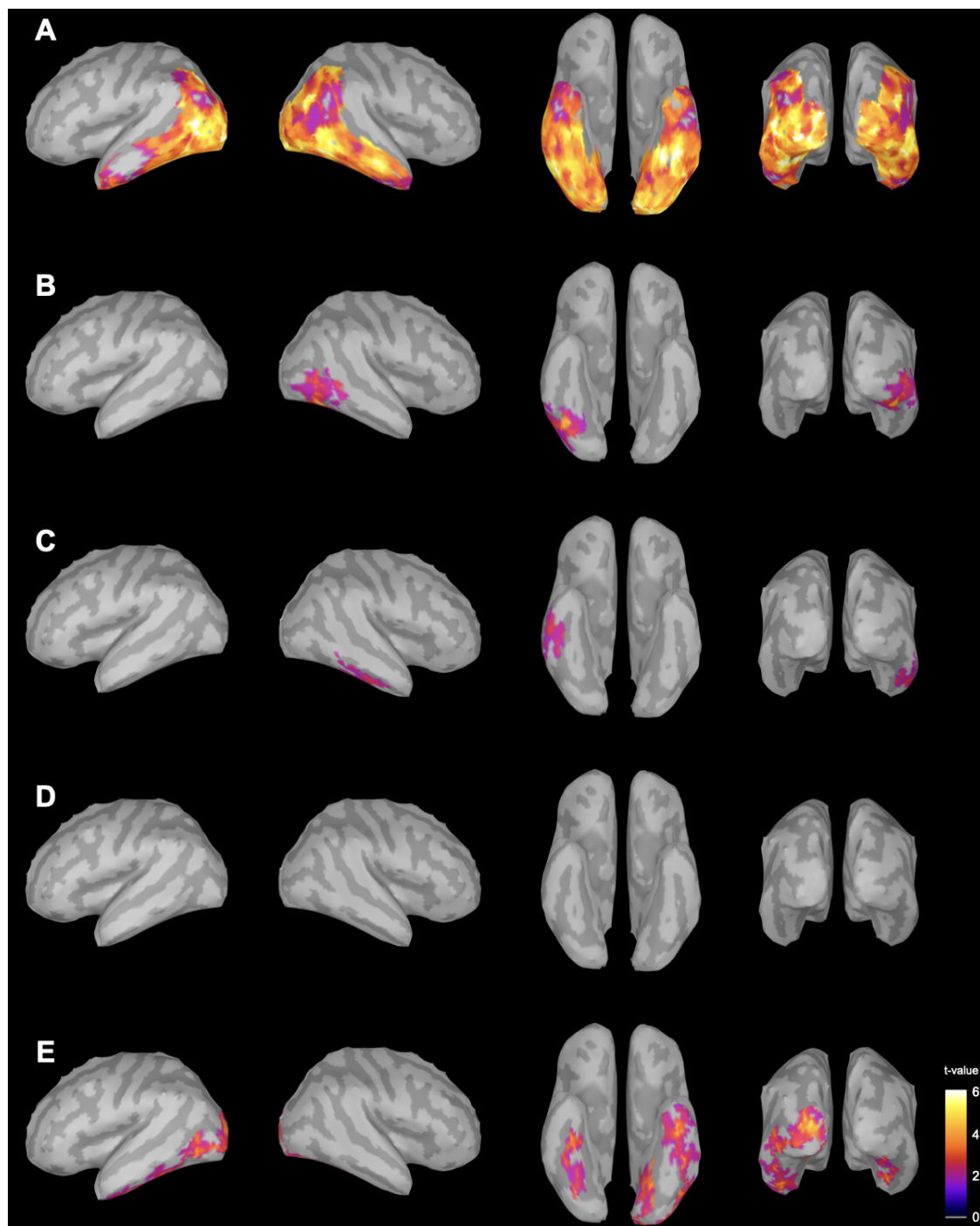
Figure 4

Source level results. Significant discrimination responses (p<0.05) for the five linguistic properties under study (from the top: (A) Alphabetic, (B) Readability, (C) Familiarity, (D) Meaningfulness, (E) Lexicality), displayed (from left to right) with left, right, ventral and posterior views.