

1 **The *What, When, Where, and How* of Visual Word Recognition**

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Abstract

A long-standing debate in reading research is whether printed words are perceived in a feedforward manner on the basis of *orthographic* information, with other representations such as semantics and phonology being activated subsequently, or whether the system is fully interactive and feedback from these representations shapes early visual word recognition. We review recent evidence from behavioural, fMRI, EEG, MEG and biologically-plausible connectionist modeling approaches, focusing on how each approach provides insight into the *temporal flow* of information in the lexical system. We conclude that, consistent with interactive accounts, higher-order linguistic representations modulate early orthographic processing, and discuss how biologically-plausible interactive frameworks and coordinated empirical and computational work can advance theories of visual word recognition and other domains (e.g., object recognition).

81 hierarchical manner, wherein orthographic representations feed into higher
82 level linguistic representations, or whether higher level linguistic information
83 such as phonological, and morphological structure exerts a top-down influence
84 on visual-orthographic processing relatively early (see BOX 2). Cognitive
85 neuroscience has rekindled this debate through the introduction of techniques
86 like EEG and MEG, which have the appropriate temporal resolution to track the
87 time course of processing. Note, however, that the '*where*,' '*what*,' '*how*,' and
88 '*when*' questions are to a large extent interdependent. The human brain is
89 generally constructed so that the trajectory of increased complexity, in terms of
90 moving from relatively simple "microfeature" representations (e.g., the line-
91 segments in a letter) to complex, higher-order representations (e.g., a
92 representation of the whole word form) is occipital-to-frontal, whereas the
93 trajectory of high-level modulation is frontal-to-occipital. Since '*where*'
94 information is correlated with the flow of processing (early/simple or
95 late/higher-order), locations of brain activations are often taken to support
96 claims regarding the temporal order of processing. Here we will discuss the
97 potential danger of using evidence of '*where*' to make inferences about '*when*'
98 (and '*how*'), review the findings that have been obtained with techniques having
99 the appropriate temporal resolution for tracking the time course of printed word
100 processing, and point to the desirable cross-fertilization between behavioural
101 data, neuroimaging techniques, and neurobiologically-plausible computational
102 models, for developing a mechanistically explicit theory of visual word
103 recognition.

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114 **fMRI evidence suitable for ‘*where*’ but not for ‘*when*’**

115 Many fMRI studies have investigated the brain circuits that underlie
116 reading. Two points on which this research converges is that left hemisphere
117 plays a major role in reading, and that the reading circuit consists of a network
118 with two major pathways: (1) a dorsal pathway including the occipital,
119 supramarginal and angular gyri, the premotor and the pars opercularis in the
120 inferior frontal cortex, and (2) a ventral pathway that integrates the left fusiform,
121 middle and anterior temporal and the pars triangularis in the inferior frontal
122 cortex [4]. This notwithstanding, there is still a heated debate regarding the
123 characterization of directionality of flow of information in these pathways (i.e.,
124 ‘*when*’ and ‘*how*’). Specifically, the literature is unsettled regarding the extent to
125 which higher-level lexical representations that are not necessarily orthographic
126 modulate the relatively early processing of orthographic information (see BOX
127 3).

128 One of the most relevant examples of such debates is the role of the left
129 fusiform gyrus, the putative *visual word form area* (VWFA) [5, 6]. From an
130 anatomical processing perspective (i.e., a ‘*where*’ distinction), this brain region is
131 considered to be a relatively “early” processing area. The left fusiform gyrus has
132 been shown to be more activated for words or pseudowords than for false fonts
133 or consonant strings [7-10]. It is thus commonly accepted that the left fusiform is

134 involved in orthographic processing. There is a controversy, however, regarding
135 what specific information is represented in this brain region and how sensitive it
136 is to top-down information. One theoretical position is that the VWFA is a
137 prelexical hub, specific for written words, that computes and stores strictly
138 visual and abstract prelexical orthographic representations in a primarily
139 feedforward manner [8, 11, 12]. Another theoretical position, however,
140 postulates that activation of the visual form area is modulated by higher-order
141 linguistic properties of the stimuli such as phonology, morphology, and
142 semantics [13, 14]. These two approaches provide very different views of
143 reading: The former is compatible with the notion of feedforward temporal (and
144 also structural) modularity (see BOX 2), wherein reading is considered to rely on
145 a sequence of consecutive brain areas sensitive to a hierarchy of orthographic
146 representations (e.g., letters, letter clusters of increasing size) that culminates in
147 the recognition of a word. The latter considers reading as a fully interactive
148 processing system wherein higher-level linguistic information that is not
149 necessarily orthographic modulates early perceptual-orthographic processing.

150 Whereas proponents of the feedforward approach have relied on the
151 argument that activation of the VWFA reflects a stage of *orthographic* processing
152 that is immune to phonological and semantic influences which come into play
153 only later on [12, 15, 16], there is mounting evidence suggesting that early print
154 processing in the VWFA is modulated by higher-levels of lexical information. For
155 example, sensitivity to high-level variables such as lexical frequency has been
156 observed in the left fusiform [17]. Furthermore, the VWFA was similarly
157 activated when target words were preceded by masked printed word primes or
158 by masked pictures [18] (see BOX 1). Note that bidirectional flow of information

185 perception and word meaning. It is this time course that provides important
186 evidence to adjudicate between different theoretical stances regarding the flow
187 of information (feedforward vs. feedback). Both techniques tap synchronized
188 neuronal activity over time triggered by some cognitive event in the brain [26].
189 Unlike RTs, which give us the end result of processing in the system as a whole
190 (and not specifically of lexical processing, see BOX 1), both MEG and EEG provide
191 a continuous measure of the intermediate events that have led to the final
192 response. MEG also provides some spatiotemporal constraints, allowing for some
193 synthesis of *'when'* and *'where'* information.

194 One of the earlier markers of visual word recognition is a left lateralized
195 N150/N170 response that has been found to differentiate orthographic stimuli
196 such as words and pseudowords from other stimuli such as symbols [27-29].
197 Selective responses to letters in this time window have also been found in the
198 inferior occipitotemporal cortex using intracranial recordings [30, 31] and MEG
199 [32, 33], particularly for normal readers but not for dyslexic children [34-37].
200 Thus, it has been proposed that the left-lateralized N170 could be an automatic
201 response related to typical visual word recognition, and that it could be
202 associated with the activation found using fMRI in the VWFA-left fusiform gyrus
203 [38](see however Rauschecker et al. [39] for bilateral effects). In fact, all this
204 evidence supports the claim that at approximately 150 ms from stimulus onset
205 the visual system responds only to the frequency of letter combinations, and that
206 lexical and phonological effects come into play much later [15, 16, 40]. As we will
207 expound below, however, higher-level linguistic information has been shown to
208 exert its influence already at 100 ms (that is, before 170 ms) from stimulus
209 onset. For instance, early ERP components in the range of 100-200 ms have been

210 reported to be sensitive to lexical frequency [41-45]. Thus, from a simple time-
211 scale perspective, an early marker of visual word recognition as revealed by ERP
212 measures (but not fMRI measures) seems to be susceptible to modulation from
213 higher-order lexical information.

214 Another early marker of reading is the N250, which was originally found
215 to be sensitive to orthographic similarity in combined masked priming and EEG
216 studies [46, 47]. However, subsequent studies have shown that the N250 is also
217 modulated by lexical factors [48, 49]. In particular, this ERP component was
218 found to be sensitive not just to letter identity but also to the phonological status
219 of the letters—that is, whether the letters are consonant or vowels [46, 50-52].
220 For example, Carreiras and colleagues [46] showed that masked subset priming
221 of consonants (e.g., mln-melon) and masked full identity priming (e.g., melon-
222 melon) do not significantly differ from each other already in the N250
223 component, whereas masked vowel subset priming (e.g., aio-amigo) and masked
224 identity priming (e.g., amigo-amigo) do significantly differ. Because consonants
225 are more lexically constraining than vowels in predicting word identity [53], this
226 effect demonstrates that top-down lexical information modulates the N250
227 component. Note that the same pattern of response is revealed in the later N400
228 component and in RTs in the behavioral experiments. This suggests that the
229 accumulated lexical information (and/or lexical competition) that is generating
230 the masked prime has exerted its full impact by 250 ms from stimulus onset. In
231 fact, the dissociation found between transposed-letter priming effects for word-
232 word pairs (e.g. ‘casual–causal’) and for nonword-word pairs (e.g. ‘barin–brain’)
233 in the N250 component [48] reinforces the hypothesis of high-order lexico-

234 semantic information constraining orthographic form-level processing in the
235 N250.

236 Consistent with a sustained and early interactive co-activation of a
237 network of sites contributing to reading, Thesen and colleagues [54] found a
238 strong phase-locking from 170 to 400 ms between the left fusiform and more
239 anterior language areas when comparing words versus false fonts using MEG
240 and intracranial recording. Other recent reports of very early neurobiological
241 responses to phonological information in anterior areas are also consistent with
242 a top-down flow of information during visual word recognition. Using MEG in a
243 masked priming paradigm, Wheat and colleagues [55-57] observed stronger
244 responses to pseudohomophones than to orthographic control primes within
245 100 ms of target word onset in a cluster that included the left inferior frontal
246 gyrus (pars opercularis) and the precentral gyrus. Note that a parallel pattern of
247 activation found in the middle occipital gyrus suggests that these regions could
248 be oscillating together during visual word recognition at a very early stage. Thus,
249 the inferior frontal gyrus may exert feedback control on regions involved in
250 lower level analysis of written words. In fact, a recent study [58] provides
251 evidence of top-down feedback from the inferior frontal gyrus to the left ventral
252 occipitotemporal cortex via dynamic causal modeling of MEG data. Specifically,
253 the researchers found that words (as compared to false fonts) activated the left
254 inferior frontal gyrus. More importantly, they showed that feedback connections
255 from the inferior frontal gyrus onto the left ventral occipitotemporal cortex
256 within the first 200 ms provided the best fit for the data relative to a model with
257 only feedforward connectivity between those regions. One possible explanation
258 for this feedback is that the inferior frontal region is sending higher-level

259 information (e.g., phonology) to constrain the representations computed in the
260 left fusiform. Alternatively (or complementarily), these two brain regions may
261 be interacting bidirectionally as part of a constraint network with as-yet
262 underspecified graded specialization across the different contributing brain
263 regions. Although the specific representations and dynamics of the frontal-
264 occipitotemporal areas remain to be fleshed out, these data clearly challenge the
265 notion of temporal and structural modularity in orthographic processing.

266

267 **Biologically plausible connectionist modeling: A platform for advancing**
268 **theories of visual word recognition**

269 From the empirical data outlined above, it is clear that substantive
270 theoretical advance will require an integrated understanding of the
271 contributions of a large set of distributed representations stored in different
272 brain regions—brain regions that are accessed (at least initially) at different
273 points in time as activity cascades throughout the brain. Connectionist modeling
274 offers a mechanistic platform that is ideally suited for these investigations
275 because it allows researchers to probe the ‘*where*’ and ‘*when*’ of visual word
276 recognition and directly relate them to the questions of ‘*what*’ (representations)
277 and ‘*how*’ (explicit computational processing mechanisms) work in concert to
278 enable the perception of written words. Moreover, models allow researchers to
279 explore the emergent properties of these systems and develop targeted
280 empirical research agendas for the future.

281 The basic capacities of connectionist networks as outlined above were
282 keenly demonstrated via the Interactive Activation model [59-61]. In this model,

283 information from low-level visual feature detectors flowed “bottom-up” to a
284 “lexical” representation of whole words, while simultaneously being able to flow
285 “top-down” from higher levels of representation. This model was thus able to
286 explain and generate predictions regarding top-down influences related to word
287 reading, such as the word superiority effect (i.e., the processing advantage for
288 letters embedded in words relative to isolated letters) [62].

289 From this work and the general mechanics of constraint satisfaction
290 systems [63], as well as the presence of bidirectional connectivity between brain
291 regions that process different aspects of a word’s representation (e.g., letters,
292 phonology, semantics), connectionist theories of visual word recognition will, by
293 default, expect and generate some degree of top-down influence for maximally
294 accurate word identification. The more critical concern, then, is if these top-
295 down influences are substantive enough to be theoretically significant and may
296 not be dismissed for reasons of parsimony [64-67]. Proficient reading also
297 involves an optimization of efficiency in addition to one of accuracy; that is, of
298 correctly reading words as quickly as possible. Thus, if a strictly feedforward
299 system could, in principle, enable highly efficient word recognition, under what
300 circumstances would the brain “choose to pay the price” of waiting for additional
301 top-down constraints because of inadequacies in a strictly-feedforward
302 signal?[68]

303 Connectionist models offer several avenues for exploring these
304 possibilities. One particularly important recent advance is the ability to
305 incorporate additional neurobiological constraints into standard connectionist
306 models (e.g., by specifying different sub-populations of inhibitory and excitatory
307 neurons) to simulate electrophysiological and behavioral responses (B. C.

308 Armstrong, PhD thesis, Carnegie Mellon University, 2012)[69, 70]. For example,
309 Laszlo and Plaut[69] showed how a model that instantiated these principles was
310 able to generate and explain electrophysiological dynamics corresponding to the
311 N400 ERP component. Additionally, they were able to advance the field by
312 offering an account of an important discrepant finding between the behavioural
313 and electrophysiological literatures: why the N400 ERP component is not
314 sensitive to the lexicality of the stimulus (e.g., words and pseudowords vs.
315 acronyms and illegal strings), whereas behavioural responses are. Specifically,
316 they showed that the initial settling dynamics, during which the prominent
317 deflection typically associated N400 ERP component was displayed, were
318 primarily driven by the orthographic wordlikeness of the stimulus (e.g., in terms
319 of its orthographic neighborhood). However, nonlinear settling dynamics in the
320 network caused a change in these activation patterns later on in processing, such
321 that valid lexical types (words and acronyms) were more active than nonwords
322 (pseudowords and illegal strings), consistent with typical behavioural lexical
323 decision data.

324 Relatedly, Laszlo and Armstrong [70] further extended this work to
325 account for how simple context effects (e.g., word repetition) modulate the N400
326 component that has been associated with lexical-semantic access. This was
327 accomplished via the incorporation of a neuron-specific fatigue mechanism so
328 that neurons that fired recently would not be able to fire at their maximum rate
329 for a brief period of time. This resulted in a reduction of the N400 component
330 amplitudes for stimuli in the semantic representation, regardless of the lexical
331 status of the string of character that was input to the network. Moreover, they
332 were recently able to generate specific predictions regarding the power-

333 frequency spectra that should be evoked by words and nonwords (Laszlo &
334 Armstrong, unpublished)—data that are increasingly influential in establishing
335 the causal links between which brain regions influence one another and the
336 temporal order (i.e., ‘when’) in which this occurs [58, 70]. (See Figure 2). The
337 result of this work was targeted insights into ‘what’ aspects of a word’s
338 representation are modulated by related context. Furthermore, this neurally-
339 inspired account therefore presented an alternative explanation for the long-
340 accepted verbal account of N400 repetition effects [71], which stated that
341 reduced N400 amplitudes resulted from an (underspecified) facilitation
342 mechanism instead of a fatigue mechanism.

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347 With such explicit models in hand, it is possible to add or subtract
348 different feedback connections and evaluate which of these models best captures
349 empirical electrophysiological data such as ERP waveform amplitudes and
350 power over time in as parsimonious a manner as is possible. These models thus
351 present an opportunity for an “experimental” approach to theoretical
352 development, by allowing for the direct assessment of the impact of different
353 theoretical assumptions. Moreover, by virtue of the domain-general nature of the
354 framework, it is possible to naturally extend these principles to the study of
355 other levels of representation. For instance, these principles can readily be
356 employed to study ERP components associated with earlier processes related to
357 visual word recognition (e.g., N170, N250) and determine ‘when’ and ‘how’ these
358 representations shape other purportedly earlier.

359 Combined with a domain-general learning theory and recent advances in
360 ‘deep’ neural networks [72], it has also recently become possible to train
361 networks with multiple intermediate “hidden” layers whose input values or
362 target outputs are not explicitly set by the experimenter. Consequently,
363 researchers can step back from explicitly specifying the exact nature of the
364 representations that are expected to mediate between a low-level visual form
365 and higher-order lexical information. Instead, they can simply specify a more
366 neutral input (e.g., a low-level visual input associated with a word in a
367 retinotopically-centered coding scheme) and observe how unsupervised
368 learning mechanics can gradually extract higher-order information such as
369 position-insensitive visual representations and intermediate representations of
370 different grain sizes [73]. This approach enables the empirical investigation of
371 whether particular intermediate representations assumed to mediate between
372 visual inputs and higher-order lexical outputs (e.g., bigrams, syllables) are in fact
373 representations that will emerge during learning.

374 Taken together, biologically plausible connectionist models are showing
375 strong initial promise in being able to provide detailed and explicit mechanistic
376 accounts of ‘*what*’ and ‘*where*’ different types of representations are stored [72,
377 73], ‘*when*’ they interact, and ‘*how*’ the processing mechanics of
378 neurobiologically-constrained computations operate the way they do. Moreover,
379 these models can be used not only as ‘process’ models of the typical mature
380 system, but can also trace the development of lexical skills and top-down versus
381 bottom-up interactivity [74], as well as seamlessly enable studies of different
382 types of reading impairments [61].

383

384 **Concluding remarks**

385 Old debates regarding the modularity—or lack thereof—of visual word
386 recognition are back again with the advent of techniques such as fMRI and
387 EEG/MEG. However, the rekindling of these debates via research using these
388 techniques offers the opportunity for unique theoretical advance that was not
389 possible via behavioural investigations alone, and also enables the investigation
390 of important new questions (see BOX 4). No longer are researchers constrained
391 to ‘black box’ theorizing regarding the internal mechanics of the brain that
392 mediate between stimulus and response. Rather, these representations can now
393 be monitored directly and used to motivate specific theoretical claims about the
394 intermediate internal representations and processes that subserve visual word
395 recognition. Like never before, it is therefore possible to achieve integrated
396 theories of ‘*what*’, ‘*when*’, ‘*where*’, and ‘*how*’ visual words are represented and
397 processed in the brain.

398

399 **BOX 1: Measuring time course in behavioural research**

400 Although behavioural investigations are useful for understanding visual
401 word recognition, these studies suffer from an inherent limitation: they only
402 provide an “end-state” reflection of the state of processing via an indirect
403 behavioural response (e.g., lexical decision time as signalled via a key-press).
404 Thus, these techniques do not provide direct insight into the internal temporal
405 dynamics underlying ‘*how*’ different representations are activated. Moreover,
406 these techniques simultaneously run the risk of producing data that are
407 contaminated by pre- and post-lexical processes (e.g., decision making).

408 These limitations notwithstanding, techniques that provide relevant indirect
409 insight into the time-course of different processes have been developed that
410 relate to the ‘*when*’ question regarding feedforward and feedback processes. In
411 this context, the masked priming technique [75] deserves special consideration.
412 In masked priming, a target word is preceded by a briefly-presented masked
413 priming stimulus (e.g., mln-melon). By manipulating the structural relationships
414 between prime and target (e.g., at the orthographic, phonological, morphological,
415 and other levels), at different exposure durations (e.g., typically between 10 and
416 60 ms), researchers have observed different time courses of processing for
417 different properties of printed words (e.g., orthographic and phonological
418 representations) [76].

419 The rationale behind this experimental approach is that the minimal prime
420 duration that is required to obtain a specific priming effect reflects the time that
421 is necessary for activating that information (e.g., orthographic, phonological,
422 morphological, or semantic information). Nonetheless this procedure has
423 limitations [77]; for instance, its lack of ecological validity. A related and more

424 ecologically-valid technique is to present the words in the context of normal
425 silent reading while the participants' eye movements are registered [78]. Here, of
426 particular interest is the very early parafoveal preview benefit effect using the
427 boundary technique in which the relationship between a parafoveal preview and
428 a target word is manipulated. Specifically, the parafoveal preview is replaced by
429 the target word once the fixation crosses an invisible "boundary" located next to
430 the target word. The differences in the fixation durations on the target word
431 caused by different structural manipulations of the parafoveal preview reflect
432 'what' information was already processed in the parafovea (e.g., orthography
433 and/or phonology and/or morphology, etc.)[79].

434 There is ample evidence that high-level information, such as phonological
435 [80, 81]; morphological [82, 83], and lexical information [84] influences very
436 early aspects of the overall visual word recognition process. This evidence
437 challenges the traditional claim of temporal and structural modularity according
438 to which printed words are principally identified on the basis of *orthographic*
439 information alone in skilled readers (the underlying logic behind some
440 researchers' conception of the VWFA), with phonological and semantic
441 information being retrieved subsequently [64, 85].

442

443 **Box 2: Structural and temporal modularity, interactivity, and orthographic**
444 **processing**

445 The main theoretical stand underlying the feedforward approach is that pure
446 orthographic models have substantial descriptive adequacy to account for a
447 large set of (mostly behavioral) data in visual word recognition [86]. One basic
448 tenet in this feedforward view is that in principle "feedback cannot improve

449 performance at either the lexical or prelexical level” (p. 306) and, indeed, a
450 number of well-known phenomena (e.g., word superiority effect) that have been
451 traditionally attributed to top-down feedback can be explained parsimoniously
452 in a feedforward manner. By this view, the game of processing printed words is
453 largely played in the court of orthographic processing, such that a significant
454 part of the recognition process is determined by considering the surface
455 structural properties of the printed stimulus alone (i.e., letters, letter sequences,
456 etc.). Interestingly, this position is consistent with the idea that the identification
457 of visual forms in general and letter strings in particular can be achieved through
458 a low-level visual pattern recognition system shared by humans and baboons
459 [87-89].

460 The strongest version of the feedforward view postulates structural
461 modularity, according to which orthographic processing is *in principle* non-
462 penetrable by other linguistic dimensions. Moreover, processing within the
463 orthographic system proceeds bottom-up from low-level features to full
464 orthographic words. The weaker version assumes temporal modularity [90], and
465 posits that the word recognition system is simply set so that the processing of
466 printed words proceeds until an orthographic word unit is recognized; only once
467 this is accomplished does the orthographic representation make contact various
468 other linguistic properties (e.g., phonology, morphology, semantics; [64]). Note
469 that this approach may allow for top-down interactivity as long as it is
470 constrained to occur after initial orthographic coding is complete.

471 The contrasting approach argues for full interactivity between lower- and
472 higher-order representations at all processing levels. Here, the demarcation line
473 beyond ‘*when*’ and ‘*where*’ “perceptual orthographic” processing ends and

474 “linguistic” processing begins is blurred [72]. By this view, high-level linguistic
475 considerations that are not purely orthographic (e.g., how some letters correlate
476 with phonology and meaning, and how letter clusters are constrained by lexical,
477 morphological, and phonological structure) shape the distributional properties
478 of letters in a given language, and the word recognition system learns these
479 features to enable efficient (i.e., fast and accurate) reading in that language.
480 Language-specific retinal-perceptual learning effects (i.e., cross-linguistic
481 difference of processing letters at different retinal eccentricities) [91] suggest
482 that reading habits stemming from the overall structure of a language indeed
483 affect the functional structure of early stages in the visual pathway, and are thus
484 compatible with this view. For example, frequently-encountered visual
485 configurations result in perceptual learning that allows for rapid and efficient
486 recognition of a word form, and these configurations are determined by the
487 correlation of orthography with phonology and meaning that are characteristic
488 to a language [92]. Because different languages are characterized by different
489 relations between orthography, phonology, and semantics (amongst other
490 representations), interactive models that allow for phonological, morphological,
491 and semantic information to come into play early on, are argued to be better
492 accounts for the substantial cross-linguistic differences observed in early
493 orthographic processing [85].

494

495 **Box 3: Future explorations of interactivity in fMRI and MEG**

496 Several studies have shown intrinsic functional connections between
497 Broca's area and ventral occipitotemporal regions [58, 93-96] Anatomical
498 connections between frontal and occipital regions through the superior

499 longitudinal fasciculus and/or the inferior fronto-occipital fasciculus have also
500 been documented [97-105]. Taken together, these findings provide the
501 neurobiological platform for possible top-down effects from frontal areas, and
502 thus offer interesting avenues for future investigations. Moreover, it is important
503 to keep in mind that readers not only activate the left fusiform and other regions
504 of the ventral pathway when reading. They also activate the dorsal pathway
505 including regions such as the left supramarginal gyrus, the left superior temporal
506 cortex, and the left inferior parietal cortex—particularly, the angular gyrus,
507 which has a modulatory effect on the visual cortex [4, 106]. Further, there are
508 other functional pathways in the reading circuit starting in the occipital cortex
509 that do not necessarily involve the left fusiform [107]. The reading circuit
510 includes not only one, but multiple pathways from vision to higher-order
511 temporal lobe language areas. Thus, the full scope of interactivity (or lack
512 thereof) between regions spanning the different pathways of the reading circuit
513 should be more fully established. Finally, it is important to note that the dorsal
514 and ventral pathways are not modular systems that operate independently of
515 each other, but exchange information during visual word recognition [108, 109].
516 In fact, structural connectivity between regions belonging to each of the two
517 pathways (e.g., the posterior inferior temporal regions, including the left
518 fusiform, and the posterior superior temporal and inferior parietal regions,
519 including the supramarginal gyrus) has been documented [110]. Moreover,
520 functional connectivity between these regions has been shown in skilled readers
521 [111] but not in dyslexic individuals [112]. Further studies are required to
522 determine how brain regions falling along the ventral and dorsal pathways

523 interact and cooperate during visual word recognition, as well as how these
524 interactions relate to other similar processes such as object recognition.

525

526 **Box 4. Outstanding questions and future directions**

527 1. How anatomical and functional connectivity, and consequently the temporal
528 flow of information, evolves from preliterate to skilled reading?

529 2. What are the functional/anatomical differences underlying reading
530 disabilities, and how their understanding can help the implementation of
531 remediation programs?

532 3. How are connectivity and interactivity modulated by different languages
533 having different scripts, different orthography-to-phonology relations, and
534 different morphological systems?

535 4. What do the constraints of possessing different orthographic, phonological,
536 and semantic representations have on visual word recognition in the case of
537 bilingual and multilingual readers?

538 5. How can more biologically plausible computational models interact with
539 empirical investigations to produce theories that are mechanistically explicit,
540 comprehensive, and parsimonious?

541 6. To what extent will a neurobiological theory of visual word recognition *that*
542 *considers the full patterns of brain connectivity and interactivity* provide insights
543 into domain-general mechanisms shared by other related abilities such as object
544 recognition?

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828 **Figure Titles and Legends**

829 **Figure 1.** Core architectural and functional assumptions of temporally-modular
830 feedforward versus interactive models of visual word recognition.

831 (a) Temporally-modular feedforward models claim that the visual-orthographic
832 information is processed in a set of distinct, hierarchically-organized processing
833 stages, such that each stage (e.g., the activation of letter and orthographic-lexical
834 representations) occurs in a strictly feedforward—and in the strongest form,
835 sequential—fashion. Critically, additional non-visual-orthographic
836 representations (e.g., phonology, semantics) are not accessed until orthographic
837 access is complete and/or if accessed before that point, higher-level
838 representations never feed back to influence the orthographic computation.

839 (b) Interactive-Activation models [59] claim that visual information continuously
840 cascades throughout the entire orthographic-phonological-lexical-semantic
841 network. This enables partially-resolved phonological and lexical-semantic
842 representations (amongst others) to feed back and provide constraint on other
843 (lower) levels of representation in the network such as orthography. Note that
844 additional intermediate levels of representation (e.g., letter-clusters) have been
845 suppressed for simplicity in both figures, and that these are but two examples of
846 each type of network (e.g., other feedforward theories suggest direct sublexical
847 input to phonology but are nevertheless feedforward). Solid blue lines denote
848 feedforward connections; dashed green lines denote feedback connections.

849

850 **Figure 2.** Integrating insights from more biologically-plausible connectionist
851 models and neuroimaging data.

852 Recent connectionist models that employ large pools of excitatory neurons and
853 small pools of inhibitory neurons (here, inhibitory sub-populations are coded by
854 a “-”, all other neurons are excitatory), as well as sparse/weak distal connections
855 (thin arrows) and dense/strong local connections (thick arrows), and emergent
856 hidden representations that are not explicitly specified by the modeler (denoted
857 by < > around the name of the approximate representation that should emerge in
858 that pool) have enabled major advances towards explaining and predicting
859 behavioural and neuroimaging data with a computationally explicit theory. For
860 example, Laszlo and Plaut [69] and Laszlo and Armstrong [70] used the
861 architecture illustrated in (a) to generate (b) simulated ERP components that
862 explained empirical ERP data from (c) an analogous experiment involving lexical
863 types including words (e.g., DOG), acronyms (e.g., DVD), pseudowords (e.g.,
864 GORK) and illegal strings (e.g., XFQ) both on their initial presentation (thick
865 lines) and when the item was repeated (thin lines). Note that the units in the
866 model data are arbitrary and are omitted; in the empirical data, the x-axis ranges
867 from 0-900 milliseconds and negative is plotted up. All empirical and simulation
868 data were drawn from Laszlo & Armstrong [70], used with permission. These
869 ERP data were collected from an electrode placed on a middle parietal location.
870 This work suggests that (d) in a more comprehensive model that also contains
871 orthographic and semantic representations (here the <o-p>, <o-s>, and <p-s>
872 labels denote intermediate pools of neurons that map between orthography,
873 phonology, and semantics, respectively), it is in principle possible to study the

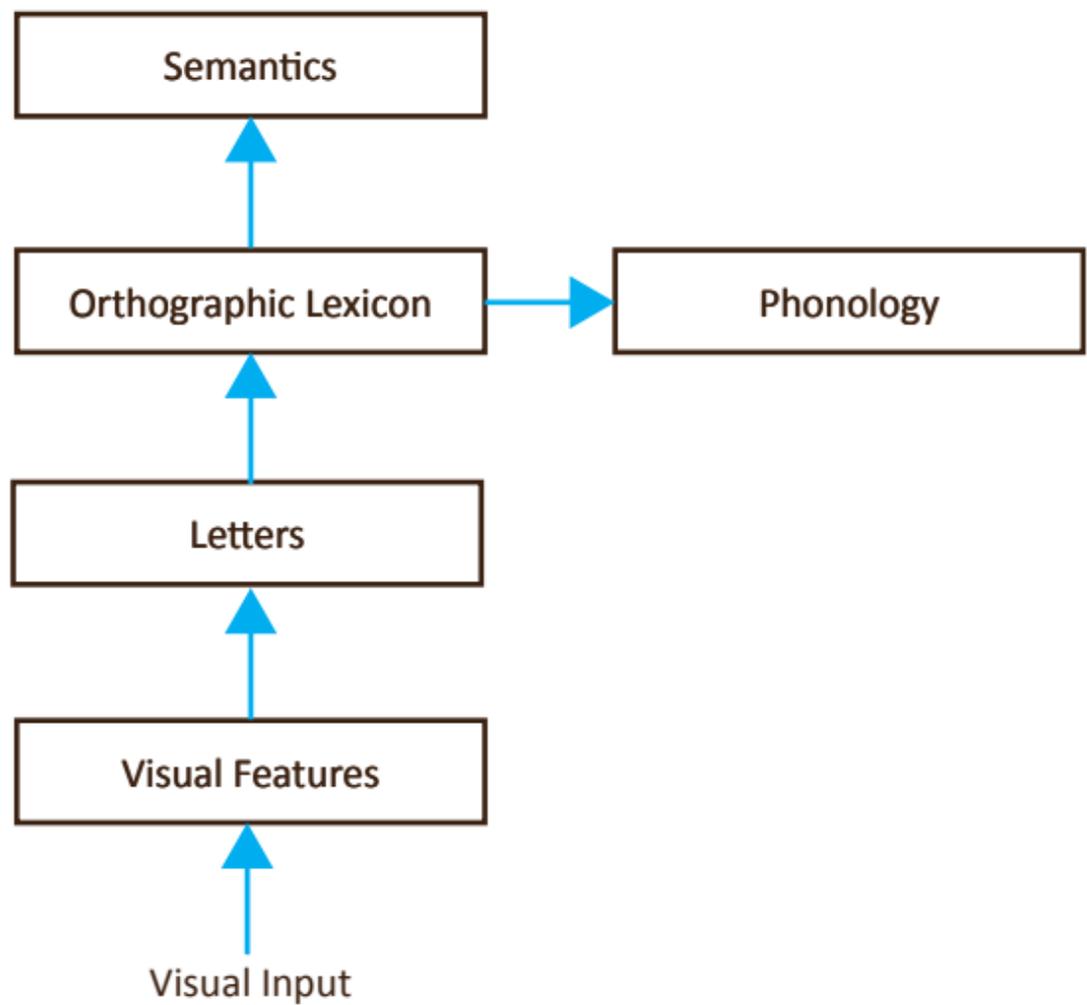
874 activation dynamics and representations that emerge in (e) brain regions
875 associated with different representations, of which a subset of the most critical
876 regions are shown in a lateral cross-section of the left hemisphere. The colour of
877 the circles denotes the theoretical representations in the model that these
878 regions might subserve. IF = Inferior Frontal Cortex; SG = Supramarginal Gyrus;
879 AG = Angular Gyrus; AT = Anterior Temporal Cortex; FG = Fusiform Gyrus
880 (includes Visual Word Form Area; VWFA); OC = Occipital Cortex.

881

882

883

a)



(b)

