

Invited Review

Task dependent lexicality effects support interactive models of reading: A meta-analytic neuroimaging review

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ARTICLE INFO

Article history:

Received 19 February 2014

Received in revised form

28 November 2014

Accepted 11 December 2014

Available online 15 December 2014

Keywords:

fMRI

Psycholinguistics

Activation likelihood estimate

Lexical decision

Naming

Parallel distributed processing

ABSTRACT

Models of reading must explain how orthographic input activates a phonological representation, and elicits the retrieval of word meaning from semantic memory. Comparisons between tasks that theoretically differ with respect to the degree to which they rely on connections between orthographic, phonological and semantic systems during reading can thus provide valuable insight into models of reading, but such direct comparisons are not well-represented in the literature. An ALE meta-analysis explored lexicality effects directly contrasting words and pseudowords using the lexical decision task and overt or covert naming, which we assume rely most on the semantic and phonological systems, respectively. Interactions between task and lexicality effects demonstrate that different demands of the lexical decision and naming tasks lead to different manifestations of lexicality effects.

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Contents

1. Introduction	148
1.1. LDT and naming task characteristics	149
1.2. Previous meta-analyses of lexicality effects	149
1.3. Summary of predictions	150
2. Material and methods	150
2.1. ALE dataset	150
2.2. ALE analysis	150
3. Results	151
3.1. Interactions between task and lexicality	151
3.2. Main effects of lexicality and task	152
4. Discussion	153
4.1. Lexicality by task interactions	154
4.2. Overall lexicality differences	155
4.3. Overall task differences	155
4.4. Implications for cross-linguistic differences	156
4.5. Implications for distributed models of reading	156
4.6. Conclusion	157
References	157

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<http://dx.doi.org/10.1016/j.neuropsychologia.2014.12.014>

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1. Introduction

Reading entails the decoding of visual orthographic representations into a phonological representation. The ease with

which skilled readers map between these very different representational systems is the product of a great deal of explicit and implicit learning. In alphabetic languages, on which we focus here, a fluent reader will have spent considerable time undertaking explicit instruction in the rules for mapping letters and letter combinations to existing verbal representations (i.e., the alphabetic principle). Models of reading development and disorders agree that phonologically decoding a particular string of letters depends on whether or not those letters map to a word with which an individual is familiar. Lexicality manipulations are consequently an important tool for investigating reading processes. Lexicality refers to whether a letter string represents a word with an associated meaning (e.g., TRAY). Letter strings that do not represent words can be either pseudowords (e.g., TAYR), which are pronounceable strings of letters sharing characteristics of legal words but without an associated meaning, or non-words (e.g., RTYA), which have no associated meaning and additionally violate the spelling rules for a language. Lexicality presumably influences many aspects of language processing and may consequently be investigated using any number of experimental tasks. Of these, however, the lexical decision task (LDT) and naming (overt or covert) dominate the neuroimaging literature (Katz et al., 2012).

1.1. LDT and naming task characteristics

In the context of orthographic processing, the LDT requires participants to indicate whether a given letter string is associated with a real word. Participants are not expected to retrieve or even possess robust semantic representations for these words, but must merely be aware that some such representation exists, and this task has consequently been described as a signal detection process (Jacobs et al., 2003). Not all models of reading agree on the degree to which the LDT relies on semantic knowledge. For example, in the dual route cascaded (DRC) model of reading aloud (Coltheart et al., 2001), lexicality decisions are based on the outcome of a lookup process in the orthographic lexicon, and may proceed even if the semantic system is removed entirely (Coltheart et al., 2010). A contrasting perspective, taken by parallel distributed processing (PDP) models, such as the triangle model (Seidenberg and McClelland, 1989) is that there are no lexicons (Dilkina et al., 2010). Rather, reading in these models is the product of the dynamic interaction of orthographic, phonological and semantic processing systems (Harm and Seidenberg, 2004). The centrality of these interactions to the triangle model of reading, which assumes that skilled reading is the dynamic product of interactions between these systems, suggests this model as a framework for their interpretation. Unfortunately, only one study to date (Harm and Seidenberg, 2004) has fully implemented the triangle model (i.e., containing semantic, orthographic and phonological representational units), and this study did not explore the interaction between task and lexicality. Within the triangle model, the presence or absence of associations between a particular orthographic/phonological pattern and a semantic representation determine the lexicality status of a token. We take the position that the LDT is, by definition, tied to semantic memory, as even in the DRC model, lexical entries exists only for a letter strings with underlying semantic representations. This position is supported behaviorally, as LDT appears to automatically activate semantic representations, if available, though this activation may decay quickly without active maintenance (Neely et al., 2010). Moreover, compared to naming, LDT performance appears to be more dependent on semantic properties of words (Balota et al., 2004; Yap and Balota, 2009). We reiterate for clarity, however, that different models make different assumptions regarding the nature and degree of support that semantic knowledge provides. Within the DRC, for example, the semantic system may provide input into the phonological and

orthographic lexicons, providing a basis for semantic priming effects in LDT and naming tasks (Blazely et al., 2005), but it is not strictly required for either task. Moreover, simulations of semantic processing in these tasks within the DRC do not exist. Thus, it is unclear whether the DRC predicts that the LDT should be particularly sensitive to semantic input.

Naming, whether overt or covert, requires participants to transform a given letter string into the corresponding phonological representation, and in the case of overt naming, or “reading aloud”, additionally generate the articulatory motor sequences required to verbalize that representation. Because the spelling-to-sound mappings for pseudowords are unfamiliar, reading aloud should be more difficult for these items. The triangle model assumes that naming taps semantic representations, and the neuroimaging literature supports this argument (Binder et al., 2005). However, we assume that naming task performance is more tightly bound to processing within the phono-articulatory system, and this too is borne out behaviorally: Balota and colleagues carried out hierarchical regression analyses of naming and LDT latencies for monosyllabic (Balota et al., 2004) and multisyllabic words (Yap and Balota, 2009). These studies, which examined the influences of phonological (e.g., onset phoneme characteristics), lexical (e.g., orthographic neighborhood size) and semantic (e.g., imageability) features show that phonological features and word length (both characteristics relevant to pronunciation) are more predictive of naming performance, whereas semantic variables were more predictive of LDT performance.

Because only words have associated semantic content, we predict increased activation for words relative to pseudowords in regions implicated in semantic processing, most pronounced for the LDT. Conversely, we predict increased pseudoword activation in phono-articulatory areas, reflecting the increased difficulty in making spelling-to-sound mapping for these items, and this should most pronounced in naming.

To our knowledge, only Carreiras et al. (2007) have explored task by lexicality interactions, finding some evidence that lexicality effects are modulated by task. Naming was associated with greater left precentral gyrus activation than the LDT for the [Pseudowords > Words] contrast, which the authors argued reflects non-semantic phonological retrieval for pseudowords. This supports the argument that naming more strongly taps phonological processes and that these activations should be stronger for pseudowords. However, the LDT was associated with greater right inferior frontal gyrus activation (IFG) for words, which they argued reflected response inhibition for pseudowords, rather than semantic activation for words. Because processes related to response selection and attention have not been modeled within the triangle model, we will not speculate on this result. Carreiras et al. did, however, find greater activity for words than for pseudowords in a middle temporal region implicated in semantic processing (Binder et al., 2009) that was numerically greater for LDT. This leaves open the possibility of a subtle task by lexicality interaction within this region, or that the items used in this particular experiment were not ideally suited for eliciting robust semantic activation. A meta-analytic review of task and lexicality effects may thus reveal semantic-processing related interactions between lexicality and task in middle temporal regions.

1.2. Previous meta-analyses of lexicality effects

Reading in alphabetic languages involves the coordination of a network of brain regions that, broadly speaking, play specialized roles in supporting orthographic, phonological and semantic processing. The role of individual or networks of brain regions underlying these processes has been studied in great deal. Orthographic processing is attributed to bilateral occipitotemporal

cortex and left mid-fusiform gyrus. Phonological processing is attributed to left superior posterior temporal cortex and the temporoparietal junction and inferior frontal gyrus extending to premotor cortex. Finally, semantic processing is attributed to anterior fusiform and inferior and middle temporal gyrus and the anterior inferior frontal sulcus. Though a thorough summary of the literature supporting these functional assignments is beyond the scope of the present article, they fall from meta-analyses of the neuroimaging literature (Taylor et al., 2013), and are also consistent with a large body of patient studies (e.g., Damasio, 1992; Schwartz et al., 2009; Turkeltaub et al., 2013).

As argued earlier, lexicality effects provide insight into the effect of word knowledge on reading, and experimental manipulations involving words and pseudowords are commonly used. Three previous meta-analyses have examined the patterns of word and pseudoword activations across multiple tasks, including naming, lexical decision, phonological decision and semantic tasks. Jobard et al. (2003) and Cattinelli et al. (2013) used anatomical label as a clustering mechanism, in contrast with the ALE approach used by Taylor et al. (2013), and in the present study, which assesses inter-study concordance by measuring co-activations within Gaussian fields. There are many ways in which words and nonwords differ, and lexicality effects can consequently be used to provide insight into many aspects of reading. The Cattinelli study aimed to further qualify the subnetworks that support different aspects of reading, and the authors argued that word and pseudoword reading depends on distinct subnetworks involved in lexical/semantic processing and in phonological/orthographic processing, respectively. Because models often make different assumptions about how lexicality influences reading, lexicality effects are often used to support or challenge these models. The Jobard and Taylor meta-analyses examined many such studies to assess whether the neuroimaging literature generally supports the DRC (Jobard et al., 2003), and test several predictions made by the DRC, connectionist dual-process (CDP+) and triangle models (Taylor et al., 2013). Though Cattinelli et al. (2013) separately examined the effects of lexicality, task and difficulty (which may also be task-dependent), none of the previous meta-analyses have examined interactions between lexicality and task.

1.3. Summary of predictions

Analyses of lexicality by task interactions would provide valuable insight into how semantic and phonological knowledge interact with the orthographic system during reading. Because these interactions have not been formally modeled in a fully-implemented simulation of the triangle model, our predictions are inferred from properties of the model discovered through related simulations, and those that are generally true of this class of connectionist models. The present meta-analysis explores task-driven interactions between semantic, phonological, and orthographic systems in the context of the triangle model of reading. There is a rich body of neuroimaging literature exploring the neural substrates of these systems. Understanding how these systems interact during reading and help constrain models of reading. We predict that task effects will emerge in brain regions implicated in semantic and phonological processing between the LDT and Naming tasks, which we assume to depend differently on semantic and phonological processing. Moreover, because words may have directly associated semantic representations, but pseudowords do not, and pseudowords should be more difficult to decode, we similarly predict that lexicality effects favoring words or pseudowords should be apparent in brain regions implicated in semantic and phonological processing, respectively. Finally, we predict that task and lexicality effects will interact additively, such that activation for naming relative to LDT will be strongest for

pseudowords, and that activation for LDT relative to naming will be strongest for words.

2. Material and methods

2.1. ALE dataset

Searches for candidate reading studies were conducted in the PubMed and Google Scholar databases for fMRI and PET studies investigating reading that employed either the LDT or overt or covert naming tasks where the terms “fMRI” or “PET” and “Lexical Decision Task” or “Naming” or “Covert Reading” or “Overt Reading” and “Pseudoword” appeared in the title or abstract. Iterative searches within the citations among candidate studies located additional candidate studies with the intention of creating a comprehensive list of studies examining naming or LDT tasks. Studies cited in recent meta-analyses looking at these tasks (Cattinelli et al., 2013; Taylor et al., 2013) were reviewed to further assure completeness of the pool of candidate studies. We subsequently filtered candidate studies to include only those that met additional criteria critical to our research question. First, we retained only those studies that examined unimpaired adults reading in their native, alphabetic, language. We excluded studies that explicitly investigated reading in multilinguals (e.g., Nosarti et al., 2010). A number of retained studies failed to report whether their participants were monolingual, however in all cases the authors of these studies made claims about reading in general, rather than in multilingual populations. Thus, we assumed that the sample compositions for these studies represented normal monolingual readers. Second, all retained studies reported whole-brain direct contrasts between words and pseudowords; we excluded those that failed to directly contrast these lexicality conditions, or did so only in the context of region of interest analyses. By including only direct contrasts between words and pseudowords, the spatial distributions associated with processing each type of item are less likely to be obscured by contrasts versus (heterogeneous) baselines. Some studies reported activation foci for contrasts at multiple significance thresholds. For example, Carreiras et al. (2007) investigated interactions between task (LDT versus reading aloud) and lexicality. The authors reported activation foci and Z-statistics for both tasks where the lexicality contrast was significant for either or both tasks, when corrected for multiple comparisons. We included coordinates only for significant contrasts between orthographically comparable words and pseudowords (i.e. non-pseudohomophones). In Carreiras et al. (2007), coordinates were reported for a right inferior frontal activation that was associated with a significant Z-score for LDT, but not naming. Thus, this activation focus was associated only with the LDT task in our analysis. The resulting dataset included 33 studies published between 1997 and 2012, of which 16 used the LDT and 17 used a naming task. 1 LDT study and 3 naming studies used PET. The ratio of PET to fMRI studies used did not differ between tasks, $\chi^2(1, N=33)=1.28, p>.25$. These studies are summarized in Table 1.

2.2. ALE analysis

[Words > Pseudowords] and [Pseudowords > Words] activation foci reported across the neuroimaging literature were analyzed using a widely used activation likelihood estimate (ALE) meta-analytic approach (Eickhoff et al., 2012). Analyses were carried out in Montreal Neurological Institute (MNI) standard space. Activation foci that were reported in Talairach standard space (Talairach and Tournoux, 1988) were transformed into MNI space using the tal2icbm transformation (Lancaster et al., 2007). Analyses were performed using GingerALE 2.3 (<http://brainmap.org/>)

Table 1
Studies used in the ALE meta-analysis.

DOI	Author and year	Language	Method	Task
http://dx.doi.org/10.1162/089892903321593108	Binder et al. (2003)	EN	fMRI	LDT
http://dx.doi.org/10.1162/0898929054021102	Binder et al. (2005)	EN	fMRI	LDT
http://dx.doi.org/10.1162/jocn.2007.19.3.433	Carreiras et al. (2007)	SP	fMRI	LDT
http://dx.doi.org/10.1162/jocn.2007.19.11.1768	Diaz and McCarthy (2007)	EN	fMRI	LDT
http://dx.doi.org/10.1162/089892902317205285	Fiebach et al. (2002)	GE	fMRI	LDT
http://dx.doi.org/10.1523/JNEUROSCI.4107-04.2005	Fiebach et al. (2005)	GE	fMRI	LDT
http://dx.doi.org/10.1016/j.neuroimage.2007.04.004	Fiebach et al. (2007)	GE	fMRI	LDT
http://dx.doi.org/10.1006/nimg.2001.0940	Henson et al. (2002)	EN	fMRI	LDT
http://dx.doi.org/10.1016/j.eplepsyres.2010.12.003	Jensen et al. (2011)	EN	fMRI	LDT
http://dx.doi.org/10.1162/jocn.2007.19.10.1584	Kronbichler et al. (2007)	EN	fMRI	LDT (Phonological)
http://dx.doi.org/10.1016/j.neuroimage.2005.06.050	Kuchinke et al. (2005)	GE	fMRI	LDT
http://dx.doi.org/10.1093/brain/122.12.2337	Perani et al. (1999)	IT	PET	LDT
http://dx.doi.org/10.1016/j.brainres.2008.03.045	Sachs et al. (2008)	GE	fMRI	LDT
http://dx.doi.org/10.1016/j.neuroimage.2009.10.082	Schurz et al. (2010)	GE	fMRI	LDT (Phonological)
http://dx.doi.org/10.1162/jocn.2007.19.11.1753	Thompson et al. (2007)	EN	fMRI	LDT
http://dx.doi.org/10.1162/jocn.2010.21502	Wooliams et al. (2011)	EN	fMRI	LDT
http://dx.doi.org/10.1016/j.neuroimage.2005.04.029	Binder et al. (2005)	EN	fMRI	NAM
http://dx.doi.org/10.1162/jocn.2007.19.3.433	Carreiras et al. (2007)	SP	fMRI	NAM
http://dx.doi.org/10.1002/hbm.20122	Dietz et al. (2005)	EN	fMRI	NAM
http://dx.doi.org/10.1162/089892999563490	Hagoort et al. (1999)	GE	PET	NAM
http://dx.doi.org/10.1016/j.bandl.2011.12.005	Heim et al. (2013)	GE	fMRI	NAM
http://dx.doi.org/10.1111/1467-9450.00229	Henson (2001)	EN	fMRI	NAM (Covert)
http://dx.doi.org/10.1002/(SICI)1097-0193(1997)5:284::AID-HBM23.0.CO;2-I	Herbster et al. (1997)	EN	PET	NAM
http://dx.doi.org/10.1016/S0093-934X(03)00403-6	Joubert et al. (2004)	EN	fMRI	NAM (Covert)
http://dx.doi.org/10.1016/j.neuroimage.2003.10.021	Kronbichler et al. (2004)	EN	fMRI	NAM (Covert)
http://dx.doi.org/10.1016/j.neuroimage.2008.08.008	Levy et al. (2008)	EN	fMRI	NAM (Covert)
http://dx.doi.org/10.1162/089892905774589190	Mechelli et al. (2005)	EN	fMRI	NAM (Covert)
http://dx.doi.org/10.1162/089892903321208196	Mechelli et al. (2003)	EN	fMRI	NAM (Covert)
http://dx.doi.org/10.1162/089892900564000	Mechelli et al. (2000)	EN	fMRI	NAM (Covert)
http://dx.doi.org/10.1016/j.neuroimage.2010.09.049	Osipowicz et al. (2011)	EN	fMRI	NAM (Covert)
http://dx.doi.org/10.1038/71163	Paulesu et al. (2000)	EN/IT	PET	NAM
http://dx.doi.org/10.1523/JNEUROSCI.3113-10.2011	Vartiainen et al. (2011)	FI	fMRI	NAM (Covert)
http://dx.doi.org/10.1016/j.neuroimage.2012.02.009	Wilson et al. (2012)	EN	fMRI	NAM

Note: DOI, Digital Object Identifier accession number; EN, English; FI, Finnish; FR, French; GE, German; IT, Italian; SP, Spanish; LDT, lexical decision task; NAM, naming or reading task.

ale/), and were performed as follows: as a first step, ALE maps were created within each task for [Words > Pseudowords] and for [Pseudowords > Words] using a Monte Carlo nonparametric test of significance with a false-detection rate (FDR) corrected significance level of $pN=.05$, with an additional cluster level significance threshold constraint of $p=.05$ over 1000 iterations. In other words, clusters, of which at most 5% of their constituent voxels would be expected to be activated by chance, were retained in each map if they were at least as large as the top 5th percentile of clusters drawn from a random distribution of voxels with a density identical to the ALE data. The second step statistically compared these simple main effect ALE maps between tasks using a Monte Carlo nonparametric test of significance using a FDR=.05 over 10,000 iterations. These contrasts identified significant interactions between task and lexicality effects in studies of normal reading, and were central to our primary goal of assessing task differences among lexicality effects. We additionally created ALE maps for the main effect of lexicality (collapsing across task) and the main effect of task (collapsing across lexicality), using a FDR corrected significance threshold of $pN=.05$ and cluster size threshold of $p=.05$, matching that used for the simple main effect maps. Approximate anatomical regions and Brodmann areas for ALE clusters were determined by locating the weighted cluster centroids within the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) and Brodmann Atlas, respectively, using the MRICron software package. Though only a single region is reported for each cluster, note that larger clusters may extend into adjacent anatomical regions.

3. Results

In this section we highlight task and lexicality effects in regions that have been extensively implicated in reading including pre-frontal cortex (Inferior and Middle Frontal Gyri), inferior parietal cortex (Supramarginal and Angular Gyri), lateral temporal cortex (Superior and Middle Temporal Gyri) and ventral temporal cortex (Fusiform and Inferior Temporal Gyri). All peaks are indicated in the tables and most peaks are illustrated in the figures.

3.1. Interactions between task and lexicality

As outlined earlier, the nature of task-by-lexicality interactions remains unclear, and our primary goal was to assess whether lexicality effects (i.e. words versus pseudowords) depended on task (i.e. lexical decision versus naming). Task-related differences for the [Words > Pseudowords] and [Pseudowords > Words] contrasts are presented in Table 2 and in Fig. 1. When contrasting words versus pseudowords, LDT was more likely to recruit left middle temporal gyrus, and a number of left temporoparietal regions, extending posteriorly from posterior middle temporal gyrus to angular gyrus and inferior parietal lobule, whereas naming was more likely to recruit right posterior superior temporal gyrus. When contrasting pseudowords versus words, LDT was more likely to recruit bilateral inferior frontal gyrus (Pars Triangularis) and a left-hemisphere cluster extending ventrally from middle occipital gyrus into inferior occipital gyrus. Naming was not more likely than LDT to recruit any region when contrasting pseudowords versus words.

Table 2
ALE foci for task-dependent lexicality effects.

Contrast	Region	BA	Volume	x	y	z	Max ALE
Words > Pseudowords LDT > Naming	l Inferior Temporal Lobe	37	1552	−61	−52	−9	3.432
	l Middle Occipital Gyrus	19	912	−39	−73	41	2.077
	l Angular Gyrus	39	688	−50	−68	26	2.251
	l Posterior Cingulate Gyrus	23	680	−4	−35	33	1.999
	l Superior Frontal Gyrus	9	472	−20	36	48	2.536
	l Middle Frontal Gyrus	9	232	−30	26	48	2.409
	l Middle Temporal Gyrus	21	104	−56	−54	11	2.506
Naming > LDT	r Superior Temporal Gyrus	42	64	63	−29	20	1.700
Pseudowords > Words LDT > Naming	l Inferior Occipital Gyrus	37	464	−40	−66	−1	2.106
	l IFG (Pars Triangularis)	45	440	−41	22	2	2.423
LDT > Naming	l Precentral Gyrus	6	96	−47	−3	28	1.920
	r IFG (Pars Triangularis)	45	64	46	22	23	1.730
	l Supplemental Motor Area	6	64	−6	3	62	1.899
	No significant clusters						
Naming > LDT							

Note: l=left; r=right; BA=Brodmann area; LDT=lexical decision task; volume=cluster volume in mm³; IFG=Inferior Frontal Gyrus; coordinates given in MNI stereotaxic space.

3.2. Main effects of lexicality and task

The significant interaction between task and lexicality effects indicates that one should interpret main effects of lexicality and task with caution. Nonetheless, we analyzed lexicality effects across tasks to replicate previous meta-analyses that included not only direct word versus pseudoword contrasts, but also contrasts versus baseline (Cattinelli et al., 2013; Jobard et al., 2003). Because

the contrasts associated with our input activation foci are mutually exclusive, the corresponding ALE clusters across and within each task were spatially distinct. Cluster extents and foci for [Words > Pseudowords] and for [Pseudowords > Words], collapsed across all tasks, are presented in Table 3 and illustrated in Fig. 2. Words were associated with reliably greater activation in left middle/inferior temporal gyrus, angular gyrus and left middle frontal gyrus. Pseudowords were associated with reliably greater

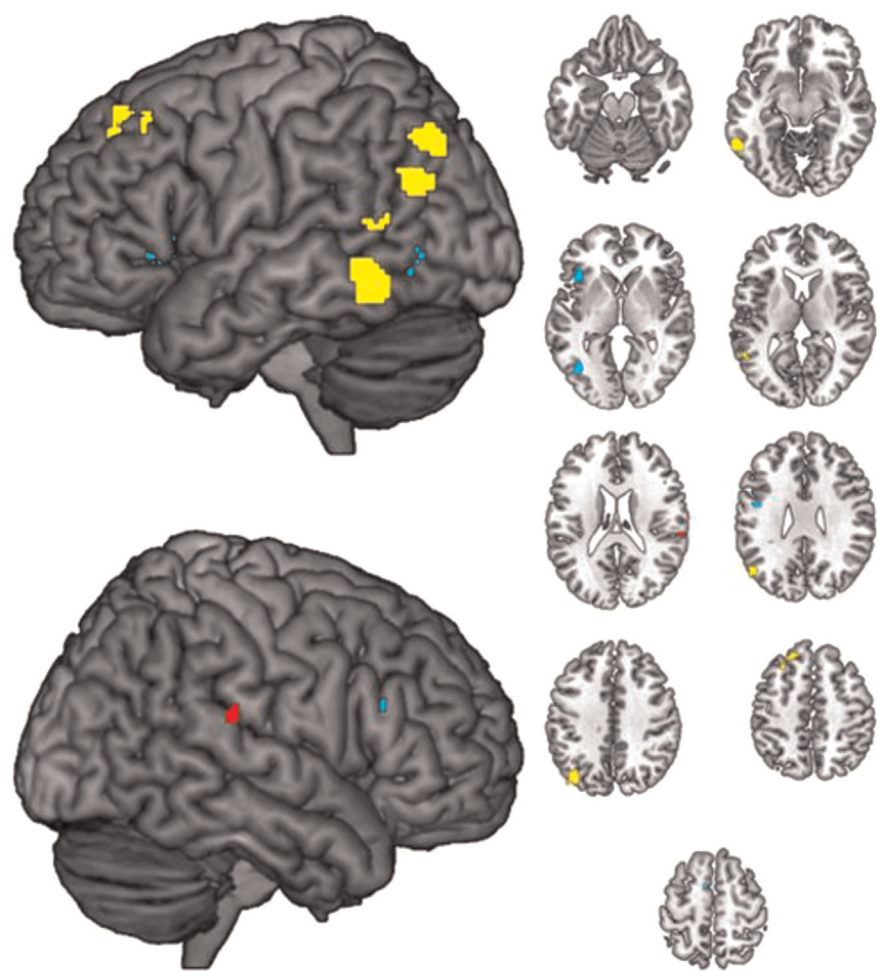


Fig. 1. Cluster-size significance corrected ALE clusters for task comparisons within Words > Pseudowords (A) showing LDT > Naming (yellow) and Naming > LDT (red) and within Pseudowords > Words (B) showing LDT > Naming (cyan). Axial slices span Z = −20 to Z = 60 in 10 mm intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
ALE foci for lexicality effects collapsed across task.

Contrast	Region	BA	Volume	x	y	z	Max ALE
Words > Pseudowords	l Angular Gyrus	39	5304	−45	−69	30	3.719
	l Middle Frontal Gyrus	8	2800	−25	25	48	3.062
	l Middle Cingulate Gyrus	23	1456	−1	−38	37	3.891
	l Inferior Temporal Gyrus	37	1064	−62	−52	−9	2.512
Pseudowords > Words	l Precentral Gyrus	6	9216	−49	3	28	3.891
	l Fusiform Gyrus	19	5728	−44	−64	−13	3.891
	l Superior Parietal Lobule	7	1504	−26	−58	47	2.807
	r IFG (Pars Opercularus)	44	1144	52	16	27	2.382

Note: l=left; r=right; BA=Brodman area; volume=cluster volume in mm³; IFG=Inferior Frontal Gyrus; coordinates given in MNI stereotaxic space.

activation in left fusiform and inferior occipital gyrus, superior parietal lobule and left inferior frontal gyrus (Pars Triangularis and Pars Opercularis).

Cluster extents and foci for [LDT > Naming] and for [Naming > LDT] task effects, collapsed across lexicality, are presented in Table 4 and illustrated in Fig. 3. Overall task contrasts revealed several clusters along a belt of cortex following the posterior middle temporal gyrus to angular gyrus and a cluster overlapping left inferior frontal gyrus (Pars Triangularis) and insula where LDT showed more reliable activations than naming. The reverse

contrast revealed small clusters in left inferior frontal gyrus (Pars Triangularis) and left cerebellum where naming showed more reliable activations than LDT.

4. Discussion

Our ALE meta-analysis examined the neuroimaging literature investigating lexicality effects using LDT and naming – two tasks that are widely used in reading research. This approach quantifies

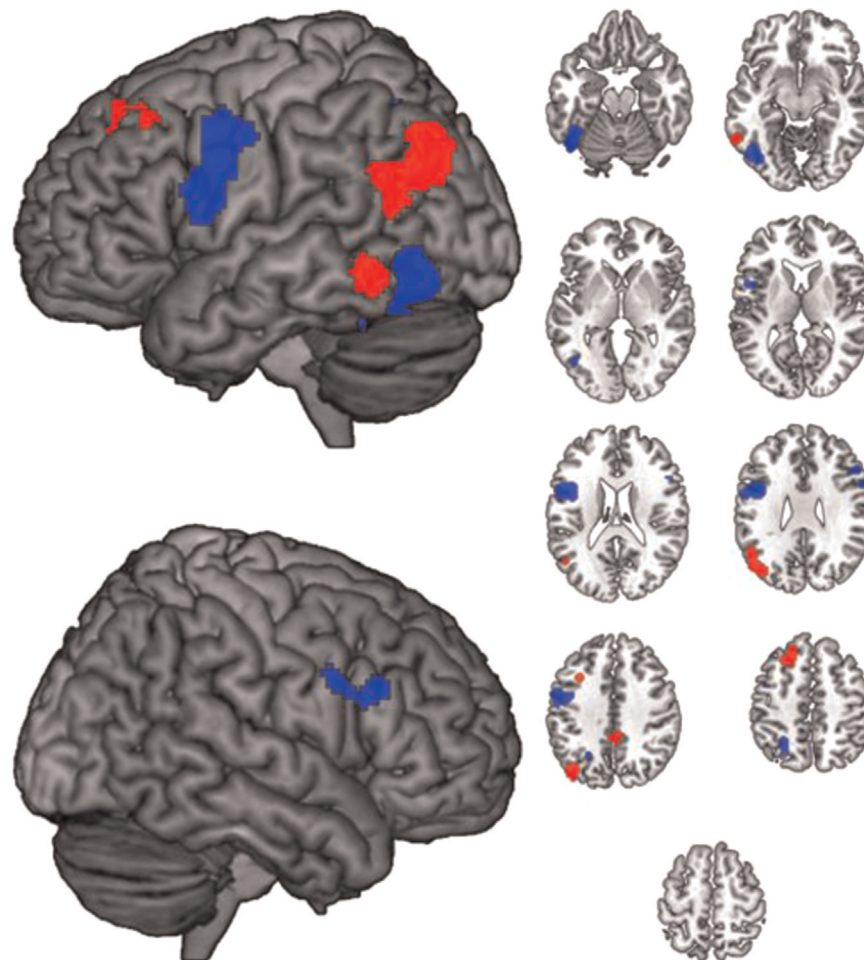


Fig. 2. Cluster-size significance corrected ALE clusters for Words > Pseudowords (red) and Pseudowords > Words (blue) contrasts collapsed across lexical decision and naming tasks. Axial slices span $Z = -20$ to $Z = 60$ in 10 mm intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
ALE foci for task effects, collapsed across lexicality.

Contrast	Region	BA	Volume	x	y	z	Max ALE
LDT > Naming	l Middle Temporal Gyrus	21	1256	−62	−52	−8	3.353
	l Middle Occipital Gyrus	19	856	−39	−73	40	2.241
	l Angular Gyrus	39	712	−50	−67	25	2.437
	l Posterior Cingulate Gyrus	23	560	−4	−35	34	1.988
	l Inferior Frontal Gyrus	47	552	−40	23	3	2.549
	l Middle Temporal Gyrus	21	448	−57	−50	9	2.484
	l Middle Frontal Gyrus	8	376	−24	21	52	2.254
	l Middle Occipital Gyrus	19	280	−40	−67	−1	2.183
Naming > LDT	l Cerebellum		72	−46	−62	−27	1.674
	l IFG (Pars Triangularis)	45	48	−51	37	3	1.825

Note: l=left; r=right; BA=Brodman area; volume=cluster volume in mm³; IFG=Inferior Frontal Gyrus; coordinates given in MNI stereotaxic space.

concordance of reported activations within neuroimaging data, showing which brain regions are reliably activated in contrasts between words and pseudowords when participants are engaged

in either of these tasks. Our primary goal, however, was to explore how task demands modulate lexicality effects, which in turn can be used to inform experimental task selection and guide the interpretation of the existing literature. Our major finding was that lexicality effects are task-dependent, and we will thus devote the next section to the discussion of these interactions.

4.1. Lexicality by task interactions

Employing multiple tasks in a single experiment increases the complexity and duration of the study. Consequently, few investigators have explored how task demands interact with neural processes in reading (Carreiras et al., 2007, 2006; Valdois et al., 2006). Our between-task comparisons therefore provide important insight into these interactions. As we argued earlier, there are clear theoretical ties between the LDT and semantic processing, and between naming and phonological processing, and that satisfactory performance on these tasks consequently places different loads on the semantic and phonological systems. Without exception, all reported behavioral data among the studies we examined indicated that pseudowords were associated with slower lexical decision and production latencies. The right inferior frontal activation for the [Pseudowords > Words] contrast may be attributable to response inhibition for pseudowords (Carreiras et al., 2007). However, we found a number of additional regions not identified by Carreiras and colleagues that also showed a greater effect for pseudowords than for words in the LDT. Lexicality decisions entail a decision component, whereas naming does not.

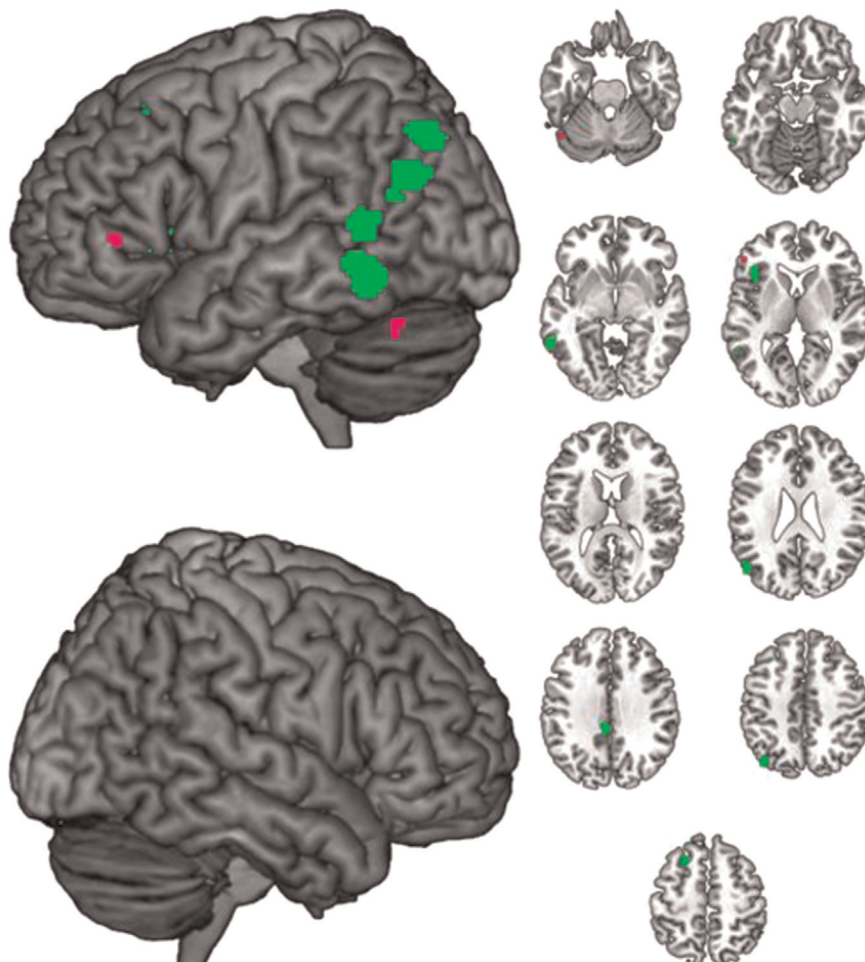


Fig. 3. Cluster-size significance corrected ALE clusters for LDT > Naming (green) and Naming > LDT (violet) contrasts, collapsed across lexicality. Axial slices span $Z = -25$ to $Z = 55$ in 10 mm intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Thus, the inferior frontal activations associated with LDT may reflect decision-related, rather than phonological processes. The Multiple Demand network, described by [Duncan \(2010\)](#) overlaps with the phonological network, and is argued to play a critical role in managing cognitive demands. Because decisions on pseudowords are assumed to be more demanding – they are associated with longer RTs – the IFG activations may correspond to the increased burden placed on this region during lexicality decisions on pseudowords, rather than from phonological processes, though the present results do not strongly support one explanation over the other.

Compared to naming, lexical decisions for the [Words > Pseudowords] contrast were more likely to produce activations within the left-hemisphere general semantic regions described in reviews by [Binder et al. \(2009\)](#) and [Noonan et al. \(2013\)](#). The left middle frontal gyrus (Brodmann area 9) activation, falls within a region that has been argued to participate in the frontoparietal control network ([Noonan et al., 2013](#)) and thus may reflect goal directed semantic retrieval for words. Activations fell within the ventrolateral region of the angular gyrus, which [Seghier et al. \(2010\)](#) argue plays a critical role in conceptual identification of visual stimuli. The posterior left middle temporal activations fall within a region often implicated in semantic processing ([Binder et al., 2009](#)), and [Noonan et al. \(2013\)](#) argue that this region is not a semantic repository, but instead involved in the strategic retrieval of semantic information, presumably represented elsewhere. In models employing distributed semantic representations, posterior middle temporal gyrus would thus act as a hub or convergence zone ([McNorgan et al., 2011](#); [Patterson et al., 2007](#)), potentially integrating information from multiple representational sources. Under this interpretation, the initiation of semantic retrieval would appear to be obligatory for known words, even during lexicality decisions, when such information is not strictly necessary for the task. Lexical decisions on pseudowords, in contrast, were more likely to activate left inferior occipital and fusiform gyrus, associated with orthographic processing ([McCandliss et al., 2003](#)), and the frontal phonological network ([Vigneau et al., 2006](#)). This pattern of activation for the [Pseudoword > Word] contrast suggests that lexicality decisions on pseudowords more strongly tax the orthographic and phonological processing systems. This would suggest that lexicality decisions do not rely solely on detecting a semantic representation, but also on input from the orthographic and phonological systems. In conjunction with the overall task effects described below, these results are consistent with the argument that lexical decisions more strongly rely on the semantic system than naming, and that words more strongly activate this system than do pseudowords because only they have semantic content. This does not imply, however, that all words should activate the semantic system equally, as not all words are associated with robust semantic knowledge ([Pexman et al., 2008](#)). Rather, it follows from the fact that words collectively have more associated semantic content than pseudowords.

Compared to lexical decision tasks, naming elicited reliably more activity only when contrasting words versus pseudowords, and only in the right superior temporal gyrus. Phonemic-level processing during comprehension and production is typically associated with left, but not right superior temporal gyrus ([Buchsbaum et al., 2001](#)), and thus this right-lateralization was not predicted. We predicted that naming would more strongly tap phonological processes, and because pseudowords should be more difficult to process, we expected that pseudoword naming would show the greatest activation in phonological processing areas, as found by [Carreiras et al. \(2007\)](#). However, assuming that this right superior temporal gyrus activity is an index of phonological processing difficulty, our results do not support this prediction. Only one study, [Hagoort et al. \(1999\)](#), contributed directly to this cluster.

Using both overt and covert naming of words and pseudowords, the authors reported left superior temporal activation for pseudowords, but right superior temporal activation for words, collapsing across naming task. Though the left superior temporal activation is consistent with our predictions, the ALE cluster to which it contributed did not reach significance in our analysis. Hagoort and colleagues do not, however, provide an explanation for the right superior temporal activation for words, making it difficult to speculate what this activation represents.

The results were inconsistent with our prediction that regions implicated in phonological processing should show the strongest effects for pseudowords during naming tasks. The lexicality effects described below suggest pseudowords are associated with an increase in phonological processing difficulty. The lack of an effect for pseudowords in the naming task was surprising, given that we had hypothesized that phonological processing should be most directly tapped during pseudoword naming. One interpretation of the pattern of interactions is that increases in phonological processing difficulty for pseudowords are similar for the two tasks. However, as noted below in our discussion of task effects, the large proportion of covert naming studies may have decreased the sensitivity of the analysis to phonological effects associated with naming.

4.2. Overall lexicality differences

The overall lexicality effects we found are consistent with recent meta-analyses by [Taylor et al. \(2013\)](#), and [Cattinelli et al. \(2013\)](#). As in these studies, greater activations for words were most reliably found in left middle temporal gyrus, angular gyrus, and inferior temporal gyrus, which are thought to be core regions of the semantic processing network ([Binder et al., 2009](#); [Taylor et al., 2013](#)). As with the [Taylor et al. \(2013\)](#) study, we found greater activation for pseudowords in the frontal phonological network ([Vigneau et al., 2006](#)) and in left superior parietal cortex, which [Taylor et al.](#) argue is involved in spelling to sound mapping. These authors suggest that these pseudoword activations reflect of the prolonged effort required to carry out spelling-to-sound mapping and compute phonological output for unfamiliar pseudowords. Unlike the Taylor study, greater activations for pseudowords were not observed in left superior temporal gyrus, which, as noted earlier, is traditionally associated with phonological processing ([Buchsbaum et al., 2001](#)), however, this discrepancy may be attributable to slight differences between the studies included in each meta-analysis. For example, because [Vigneau et al. \(2005\)](#) examined passive reading of nonwords (rather than pseudowords), it was excluded from our study, though it was included in [Taylor et al. \(2013\)](#). Similarly, [Taylor et al. \(2013\)](#) included studies such as [Tagamets et al. \(2000\)](#), and ([Xu et al., 2001](#)), which we excluded because they used neither lexical decision nor naming tasks.

4.3. Overall task differences

As predicted, LDT was more likely than naming to recruit regions implicated in lexical semantic processing. Behavioral studies have shown that, though semantic variables appear to influence both LDT and naming performance, LDT behavioral performance appears to be more strongly related to semantics ([Balota et al., 2004](#)), which our findings support. Interestingly, the significant clusters for LDT appeared to be a subset of those comprising the network derived from all semantic contrasts in the ALE analysis by [Binder et al. \(2009\)](#). However, the distribution of these clusters is also quite similar to those in the task by lexicality interaction, where the most reliable activation for words in the LDT falls within the middle temporal/angular gyrus region. This suggests

that the overall task differences in the semantic network are primarily driven by lexicality decisions for words, and not equally by both lexicality decisions.

Naming was more likely than LDT to be associated with significant activations in two clusters located in left inferior frontal gyrus and left cerebellum. Because these regions are implicated in phono-articulatory planning and motor execution, the results for the contrast of naming versus LDT is consistent with the behavioral literature showing a reliance of naming on articulatory variables (Balota et al., 2004; Ferrand et al., 2011). Overall, however, the activations associated with naming were weak. Mapping between orthographic and phonological representations should entail similar processes for overt and covert naming, and thus recruit many of the same brain regions. However, direct contrasts between the two response modalities by Palmer et al. (2001) showed that, though overt and covert responses have a similar spatial distributions, covert responses were associated with weaker response magnitudes. One interpretation of the overall task differences might be that the LDT is more cognitively demanding, however, this pattern may also reflect that a large proportion of the naming studies in our analysis employed covert naming, and thus would have shown weaker effects.

4.4. Implications for cross-linguistic differences

Our analyses looked exclusively at studies involving alphabetic languages, in which there exist mappings between orthographic and phonological word forms, the regularity of which depends on orthographic depth (Bentin and Frost, 1987). Among all such languages, the relationship between word form and semantic meaning is far less regular (ignoring for a moment the important cues that morphemic information may provide). That is, in languages with transparent orthographies, the printed form of a word is a perfect cue to its pronunciation (and vice versa), and even in languages with opaque orthographies that contain many exception words, there is nonetheless a great deal of consistency among letter-sound correspondences. However, among transparent and opaque languages alike, one cannot infer from the meaning of, for example, CAT the meaning of a word with similar orthography and phonology that does not share the same morphemic root, such as SAT. Among the studies we reviewed, a task by lexicality interaction emerged, showing LDT for words tapped the semantic system most strongly. We argue from the pattern of main effects for task and lexicality that this interaction is the result of the additive effects of task sensitivity and lexicality dependency on semantic knowledge. That is, though task demands and lexicality are individually sufficient to dictate the extent of semantic processing (as indicated by the main effects), these factors may contribute additively towards semantic processing, such that they have a greater influence on semantic processing in combination than either of them have in isolation (as suggested by the interaction). In logographic languages, such as Chinese, however, the orthographic forms of many words cue their meanings, and in such languages, a different relationship may exist.

When parafoveal information about an upcoming word is available, reading time for that word is facilitated when it is the next fixation target (Rayner, 1975). In alphabetic languages, this preview benefit does not extend to semantic processing. That is, a semantic relationship between the foveated and parafoveal word does not influence initial fixation duration when the parafoveal word becomes foveated. Rayner et al. (2003) take this lack of preview benefit in alphabetic languages to suggest that semantic activation in these languages comes after orthographic processing. Using these same eyetracking measures, Yan et al. (2009) found Chinese, but not English, readers enjoyed a semantic preview benefit (i.e., shorter fixation times) for parafoveal words. This

suggests orthographic information more quickly and directly activates semantic knowledge in logographic languages than in alphabetic languages, without the need for first phonologically decoding the word.

Despite the potential cross-linguistic differences in the directness with which orthography is mapped to semantics, reading in logographic and alphabetic languages appear to otherwise place similar demands on the reading system. Chee et al. (2000) found that bilingual English/Mandarin readers recruited left middle temporal/fusiform gyrus and left prefrontal gyrus (Pars Opercularis) when making semantic relatedness decisions to either Mandarin characters or English words. The authors concluded that processing written Mandarin otherwise resembles reading in alphabetic languages more than it does identifying pictures. Similarly, Chinese readers familiar with Pinyin (a writing system for transcribing Mandarin phonemes into the Latin alphabet) engage comparable networks when making lexicality decisions to items presented in Mandarin or Pinyin (Chen et al., 2002). Functional MRI investigating the neural substrates of word naming shows that English and Chinese show word regularity effects in a similar network of regions (Tan et al., 2001).

Wu et al. (2012) provides an overall picture of semantic and phonological processing in Chinese in their recent meta-analysis of fMRI studies. The authors separately analyzed studies using semantic and phonological tasks, respectively (four of 11 phonological tasks were naming tasks), and concluded that the network recruited for Chinese character processing was generally comparable to that typically recruited for alphabetic language processing. One notable exception was that semantic, phonological and orthographic processing in Chinese tended to recruit bilateral fusiform gyrus. Though these activations were left-hemisphere dominant and thus left-lateralized, reading in English most reliably activates only left fusiform (Wu et al., 2012), though laterality in English is likely a matter of degree, as several authors have found bilateral fusiform activation in English readers (e.g., Seghier and Price, 2011; Taylor et al., 2014).

To summarize, reading in alphabetic and logographic languages appears to rely on similar neural processes. Though our analyses were restricted to alphabetic languages, it is reasonable to expect that these results apply to logographic languages, however early automatic semantic activation in such languages may moderate potential task differences in semantic activation.

4.5. Implications for distributed models of reading

One challenge for distributed models is that they must explain how the same learning process that leads to increased semantic activation for familiar items (i.e., Words > Pseudowords), but decreased phonological and orthographic activation for the same items, as seen in the significant [Pseudowords > Words] contrast effects in left fusiform, precentral and inferior frontal gyri. Increased pseudoword activation in the phonological and orthographic system is predicted by models with attractor dynamics, such as those used in implementations of the triangle model by Harm and Seidenberg (1999, 2004). In these models, experience with regular patterns leads to the development of attractor basins, which are points in multidimensional (e.g., phonological or semantic) network state space to which nearby points are drawn (Plaut and Shallice, 1993). Attractor basins inhibit activations of unfamiliar pattern elements (e.g., incompatible phonemic combinations, but also combinations that are not frequently encountered) and excite those for familiar pattern elements. This predicts that words should show less activation than pseudowords in orthographic and phonological systems. However, as other models also predict greater phonologically-related activation for pseudowords than words (see, for example, Taylor et al., 2013), our

results do not therefore support the triangle model of reading over other models.

As indicated earlier, only [Harm and Seidenberg \(2004\)](#) have fully implemented the triangle model to date. They used this model to investigate the individual and joint contributions of the orthography–phonology–semantic and orthography–semantic pathways in a number of reading phenomena, including interactions between word frequency and regularity, and main effects of imageability and homophone and pseudohomophone reading. Though they simulated pseudoword reading (Simulation 4), demonstrating that the model was capable of inferring phonological representations for novel orthographic patterns, this simulation did not contrast pseudoword and word reading. Moreover, lexicality decisions were not simulated in the model, precluding any examination of task-by-lexicality interactions. Explorations of reading within a distributed framework would thus benefit greatly from models that permit simulations of interactions between task and lexicality among orthographic, phonological and semantic representations. Our results suggest phenomena for which neurologically plausible distributed computational models of reading should account.

Though there are many orthographic, phonological and semantic representational schemes from which one must choose for a computational model, many are relatively straightforward to implement. For example, both the [Harm and Seidenberg \(2004\)](#) implementation of the triangle model and the DRC model maintain letter-level orthographic representational units, allowing words to be composed of combinations of single-letter activations. Similarly, [Cree et al. \(2006\)](#) implemented semantic representations of concrete objects (e.g., ROBIN) as combinations of features (e.g., (has wings), (eats worms)) derived from feature production norms ([McRae et al., 2005](#)). The implementation of a cognitive task in these models, however, is much less straightforward. Task simulations entail considerations such as computational tractability, interpretability, and the complexity of orchestrating the many sub-processes entailed in even the simplest cognitive tasks. To simulate a task computationally, a researcher may have to choose among multiple possible implementations, and make simplifying assumptions about task characteristics and computational parameters. Though there may be disagreement about the chosen parameters, one advantage of formal models is that they make these decisions explicit, fostering further discussion and research regarding the validity of these assumptions ([Hintzman, 1991](#)). Because lexicality-by-task interactions have not yet been investigated in distributed models, it is unclear how this pattern of interactions would be explained within that paradigm.

4.6. Conclusion

We presented a meta-analysis of the neuroimaging literature examining the effects of lexicality among studies using lexical decision and naming tasks. We found that processing pseudowords is more strongly associated with activations in regions associated with phonological and orthographic processing, and that this lexicality effect is greatest during lexical decision tasks. We found that processing words is more strongly associated with activations in regions associated with semantic processing, and that this lexicality effect is greatest during lexical decision tasks. Understanding interactions among orthographic, phonological and semantic systems has important methodological and theoretical implications: Neuroimaging experiments investigating reading do not typically use both LDT and naming tasks. The dependency of lexicality effects on task would imply that task selection should align with the hypothesis to be tested, and that interpreting lexicality effects should account for task.

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